ENVIRONMENTAL CONTROLS OF FISH GROWTH IN THE SOUTHEAST BERING SEA

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ENVIRONMENTAL CONTROLS OF FISH GROWTH IN THE SOUTHEAST BERING SEA

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Abstract

Environmental controls of fish growth in the Bering Sea were investigated by examining growth increments and length-at-age. A sea ice-initiated conceptual model of growth that differentiates between food and water temperature controls was proposed. The timing of ice retreat in the region was hypothesized to control food availability by influencing the fate of primary production and inversely affecting prey availability in pelagic and benthic environments. The extent and persistence of ice coverage was hypothesized to influence shelf water temperatures through 'cold pool' development.

Utility of the conceptual model was assessed through regression and correlation analyses of the growth of two representative pelagic feeding species, walleye pollock and Pacific herring, and two benthic feeders, yellowfin sole and rock sole. The usefulness of herring and rock sole as indicator species of their respective feeding guilds is lessened due to feeding location and diet breadth, respectively. Food availability was shown to be the primary control of fish growth as evidenced by the growth model results of pollock and yellowfin sole and inverse size-at-age time series of these two species. The ecosystem implications of differential fish growth were assessed through investigation of the relationship of growth to condition factor and recruitment.

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Introduction

Fish growth rates are important indicators of the biotic response of fish to environmental variability. Differential growth affects recruitment and stock abundance (Ware, 1985; Bailey et al., 1996) through changes to juvenile mortality, age-at-maturation (van der Veer et al., 1994), and fecundity (Teshima et al., 1989; van Beek et al., 1989; Campana, 1996). Such changes in biology can affect management strategies considerably by altering biomass and stock recruit estimates (Fargo and Kronlund, 2000, Walters and Wilderbuer, 2000). Changes in the size-at-age can also affect gear selectivity (Winger et al., 1999; Mous et al., 2002).

Growth of fish is a function of food ingestion, assimilation, and metabolism (Jobling, 1993). As such, growth is influenced by food availability, which can limit ingestion rates at low prey densities (Smith et al., 1991), and temperature, which can influence food ingestion and assimilation rates as well as metabolic rates (Jobling, 1993). Both food availability and temperature are reflective of changes to the fish environment. The environmental influence on growth is well documented for North Atlantic groundfish (Brander, 1994, 1995; Krohn et al., 1997; Shelton et al., 1999), with the majority of this work suggesting that temperature is most important in explaining growth rate variability. However, stock biomass (Ross and Nelson, 1992) and food availability (Krohn et al., 1997) are also important, especially in single-stock studies.

The interest in growth rates of Bering Sea fish species has increased in recent years (Clark et al., 1999; Walters and Wilderbuer, 2000; Akira et al., 2001), though most work has focused on larval growth or density-dependent effects on mean size-at-age. To date, no large-scale studies in the Bering Sea have concentrated specifically on the influence of environmental factors on growth rates, nor have they extended the results to consider the impact of differential growth on the larger ecosystem. This paper addresses the effect of environmental factors on growth rates of walleye pollock *(Theragra chalcogramma)*, Pacific herring (*Clupea pallasi*), yellowfin sole (*Limanda aspera*) and northern rock sole

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(*Lepidopsetta polyxystra)* in the southeastern Bering Sea between 1982 and 2000 and considers the resultant ecosystem implications.

Conceptual model

The oceanographic environment and processes of the southeast Bering Sea are critical to understanding the environmental controls of fish growth. The region is characterized by a broad, shallow shelf extending approximately 500 km from the coast with a shelf break occurring around the 170 m isobath. The shelf contains three hydrographic fronts: outer (occurring at the 200 m isobath), middle (100 m isobath) and inner (50 m isobath) (Fig. 1). These fronts divide the southeastern Bering Sea shelf into three distinct oceanographic domains: outer, middle, and inner shelf (Schumacher et al., 1979). Vertical mixing occurs across the shelf from wind and tidal influences, with top-to-bottom tidal mixing maintaining an unstratified inner shelf (Iverson et al., 1979). Seasonal sea-ice cover over at least part of the shelf is a regular occurrence. During years of heavy ice coverage, ice extends out to the 100 m isobath, covering all of the middle and inner shelves of the southeast Bering Sea. Only a northern fraction of the middle and inner shelf are covered during years of light ice coverage (Wyllie-Echeverria and Wooster, 1998).

Sea ice plays an important role in regulating shelf water temperatures as well as shelf productivity. Spring melt of sea ice causes the formation of low salinity surface water resulting in a stratified two-layer water column over the middle shelf. The combination of a low-salinity layer, warming surface waters, and slow currents trap the winter-formed, cold water below the pycnocline (Wyllie-Echeverria and Ohtani, 1999), inhibiting downward heat transport from the overlying surface waters (Coachman, 1986). These residual winter conditions are known as the 'cold pool', which is characterized by both the temperature (<2.0°C) and salinity (32 psu) of the middle shelf bottom waters and can extend 30 to 70 m above the bottom. By this process, the seasonal sea-ice extent accounts for approximately 44% of the variability in bottom-water temperatures of the middle

shelf (Wyllie-Echeverria and Wooster, 1998), with stronger expression of 'cold pool' conditions in years of heavy ice coverage.

The timing of ice retreat influences the timing and fate of primary production. From analysis of primary production at mooring M2 on the middle shelf (Fig. 1), distinct patterns in the timing of ice retreat and type of spring bloom are evident (Stabeno et al., 2001). When seasonal ice retreat is early (prior to mid-March) spring blooms do not occur until May or early June when the water column becomes thermally stratified, with water temperatures ranging from 2.2° C to 5.1° C. When ice retreats after mid-March the bloom forms in April and May in the low-salinity melt waters of the retreating ice edge in water temperatures ranging from -1.7° C to 1° C. Early, ice-edge initiated blooms can be substantial, contributing a substantial fraction of the total shelf annual primary production (Niebauer et al., 1995). An examination of pre-1995 ice charts and observations of primary production support the above production paradigm for the southeast Bering Sea (Hunt et al., 2002). The critical dates of retreat noted above are site-specific to mooring M2 and likely increase with latitude in response to solar irradiance.

The timing of ice retreat impacts subsequent secondary production through a match-mismatch mechanism between prey and a metabolically favorable environment for zooplankton. The warm water temperatures coinciding with late spring blooms occurring after early ice retreat should increase zooplankton ingestion, maturation and growth rates (Toda et al., 1987; Ikeda, 1990; Iguchi and Ikeda, 1995), as evidenced in zooplankton biomass in the Bering Sea during warm and cold years (Smith and Vidal, 1986; Coyle and Pinchuk, 2002) and cross-shelf comparisons of copepod grazing efficiency (Cooney and Coyle, 1982). Theoretical calculations predict at least a 2-fold increase in copepod production rates when water temperatures vary by as little as 3° C (Hunt et al., 2002). Empirical evidence from a sediment trap at the M2 site supports the conclusion that zooplankton-phytoplankton coupling is greater during years of early ice retreat (Smith, 2003). The timing of retreat has been theorized to control pelagic and benthic ecosystem production by controlling the fate of surface primary production. When ice retreat occurs early in the spring, zooplankton production is increased and a pelagic ecosystem is

favored. When ice retreats late in the spring, the bulk of the ice-edge production sinks to the benthos unconsumed, fueling a benthic ecosystem (Walsh and McRoy, 1986).

Wind mixing further enhances total shelf production. Spring blooms remove nutrients from the waters above the pycnocline, and water column stability can prohibit nutrients in deeper waters from reaching the photic zone. Wind mixing in mid-to-late May replenishes nutrients in the photic zone and can prolong the bloom into summer (Sambrotto et al., 1986). Increased summer (June and July) winds can also amplify total shelf productivity (Stabeno et al., 2001) provided mixing is not inhibited by thermocline strength (Eslinger and Iverson, 2001). The amount and timing of spring and summer wind mixing, in conjunction with thermocline strength, can influence the amount of new production as well as food available to higher trophic levels (Hunt et al., 2002).

This paper proposes a conceptual model of relationships between fish growth and biophysical processes in the southeastern Bering Sea based on the ecosystem dynamics. Often a better understanding of ecosystem functioning can be inferred by treating groups of similar species as 'super species' or guilds (Austen et al., 1994). The concept of trophic guilds has been applied to the southeastern Bering Sea, dividing fish species into offshore pelagic fish consumers and inshore benthic infauna consumers (Livingston et al., 1999). Trophic guilds were modified in this study to create more basic groups: those that consume pelagic prey and those that consume benthic prey. Only those species for which annual size-at-age data were available were used. Based on common prey items, walleye pollock and Pacific herring comprise the pelagic consumers guild and yellowfin sole and northern rock sole represent the benthic consumer guild (Table 1).

The sea-ice initiated growth model (Fig. 2) includes two general hypothesized mechanisms of growth control: food and temperature. First, food availability to the pelagic or benthic environments is mediated by the timing of sea ice retreat. Through the influence of ice retreat on phytoplankton-zooplankton coupling, the model predicts that pelagic and benthic consumers will respond to sea ice retreat and resulting production dynamics in an opposite manner if food is the primary growth limitation. During years of early ice retreat the growth rate of the pelagic feeding guild should be greater compared

to years of late ice retreat and the growth rates of the benthic feeding guild should increase during years of late ice retreat. The food pathway of the model also considers the effects of wind mixing on pelagic production and the importance of stock size on growth rates via intraspecific competition (Ross and Nelson, 1992; Walters and Wilderbuer, 2000). The second hypothesis assumes that sea-ice will mediate growth through temperature via 'cold pool' development over the middle shelf. As the four species examined here inhabit the middle-to-northern extents of their range (Mecklenburg et al., 2002), temperatures are expected to be below optimum temperatures for the individual species, with growth for both pelagic and benthic consumers increasing during years of warmer water temperature.

In this paper the growth-control hypotheses is tested using growth data from the period 1982 to 2000. Stepwise-selection regression procedures are used to select significant explanatory variables from a pre-determined list outlined in the conceptual model. A similar method has been employed on growth of North Atlantic groundfish (Ross and Nelson, 1992). Additionally, ice-influenced growth models are developed to test ice-control hypothesis central to the conceptual model. These models assume that ice conditions control fish growth through control of both the temperature and food environments. Regression analyses of annual growth increments and comparative observations of mean juvenile length-at-age information are utilized to complement the regression models. The relationship of growth to condition factors and recruitment patterns are also examined to ascertain the larger ecosystem impacts of differential fish growth.

Methods

Stepwise growth models

Variable Selection

Variables were restricted to those that were either causal or modified important oceanographic conditions capable of influencing fish growth based on the assumptions of

the conceptual model (Fig. 2). Continuous time-series were preferred for constructing explanatory models and testing of functional relationships. For some variables, such as phytoplankton productivity, detrital sedimentation rates and benthic infauna biomass, continuous data sets were non-existent, or so restricted in their spatial coverage as to be of limited use. To extend the applicability of this work, variables were sought that had been used previously. However, to ensure that the most appropriate index of a given process or condition was chosen, all variables were screened for accuracy and relevancy in approximating shelf conditions prior to inclusion in the statistical models, regardless of past usage.

Size-at-age data and growth estimates

Groundfish size-at-age data was obtained from the National Marine Fisheries Service bottom trawl surveys conducted annually in the southeastern Bering Sea (Gary Walters, NOAA/AFSC, Seattle, WA, pers. comm.). The survey area covered approximately 463,000 km^2 of the Alaskan continental shelf from St. Matthew Island south to the Alaskan Peninsula (Fig. 1). Each year, the survey was conducted between late May and early August beginning from inner Bristol Bay progressing westward to the shelf edge (200 m isobath). Fish size-at-age was determined by combining otolith-derived age data and the corresponding fish lengths with species length frequencies determined from all trawls, producing a survey length-at-age distribution. From the length-at-age distributions mean length-at-age data were determined for each age class. A more detailed description of the survey methods and mean length-at-age determination can be found in Walters and Wilderbuer (2000). A 20-year (1982-2001) size-at-age time series was available for walleye pollock and 19-years (1982-2000) of data were available for the two flatfishes species, yellowfin sole and rock sole.

A 20-year time series (1982-2001) of Pacific herring mean size-at-age information was obtained from the Alaska Department of Fish and Game (Fred West, ADF&G, Anchorage, AK, pers. comm.). Data were collected from late April to May from test and commercial purse seine fisheries as well as the commercial gill net fishery of the Togiak

herring stock. Herring mean size-at-age was determined directly from raw data, as only aged fish were included in the data set. Both lengths and weights were recorded annually for aged Pacific herring, and both size indices were used in the herring growth regression analyses.

Yearly fish growth was estimated from annual cohort mean length-at-age increments for all four species as well as weight-at-age for herring. These estimates were calculated as:

$$G_x = (L_{x+1} - L_x)/t \quad (1)$$

where G_x is the absolute growth rate (mm/yr) in year X, L_x is the mean length-at-age in year X, L_{x+1} the mean length-at-age in year X + 1 and t is the time interval. Growth increments have been used previously for testing the environmental influence on growth of Atlantic cod, *Gadus morhua* (Krohn et al., 1997; Shelton et al., 1999). Because sample collection took place early in the oceanographic summer, the majority of annual fish growth was assumed to have occurred post-collection period. Such an assumption is supported by previously published work on pollock in the Bering Sea (Maeda, 1972) and yellowfin sole in the Gulf of Alaska (Paul et al., 1993). Because herring collection began prior to the feeding period (Fritz Funk, ADF&G, Juneau, AK, pers. comm.) herring growth increments accurately reflect mean annual growth, which is likely synchronous with feeding.

Minimum ages for all four species included in the analyses were determined by a combination of gear selectivity and sufficient yearly data. Maximum age was set as the age when the ratio of the mean growth over the study period to the growth standard deviation was < 1. The range of ages included in the analyses were: pollock, ages 2 to 8; herring (length), 4 to 11; herring (weight), 4 to 9; yellowfin sole, 3 to 12; and rock sole, 3 to 9. In addition to age-specific growth increments, the average annual species growth was calculated by averaging the standardized growth increments of all ages. Standardization was accomplished by subtracting the mean growth response of the

particular age from annual growth and dividing by the standard deviation (Neter et al., 1996).

Prior to performing regression analyses on growth it was determined if sexes and regions should be considered separately or if a single population for each species would be adequate. Single factor ANOVA tests were performed for all age classes of yellowfin sole, rock sole and herring to assess the magnitude of sexual growth differences. Sexual differences in mean lengths-at-age (Kuznetsova, 2000), as well as regional north-south differences (Ianelli et al., 2002) have been reported for some stocks of walleye pollock, suggesting both sexual and regional growth differences. Two-factor ANOVA tests were run on pollock testing for sex and regional growth differences with an interaction term included.

Sea ice conditions

Because of the central role of sea ice in both the food and temperature hypotheses, ice indices were sought that provided information on both the spatial (surface area) and temporal (timing of retreat) coverage of seasonal ice in the region. Both southernmost extent, defined as the latitude of furthest south advance of the ice edge along meridian 169°W, and timing of ice retreat, defined as the week of the year ice retreat begins in spring when the change in ice extent exceeds 0.5° of latitude measured along the same meridian, had been used previously by Wyllie-Echeverria (1995). To complete the 1982 to 2000 time series, digital ice charts for the region were obtained (Arctic Climatology Project, 2000, National Ice Center, Internet address: http://www.natice.noaa.gov). All digital ice charts had a resolution of at least 0.25 decimal degrees (dd). Ice-chart pixels were classified as ice covered if the ice concentration in the region was ≥ 30% (Wyllie-Echeverria, 1995). Using the same definitions of maximum sea ice extent and timing of ice retreat given in Wyllie-Echeverria (1995) the variables were recalculated for the entire study period using ArcView and ArcGIS geographic information system (GIS) software (Environmental Systems Research Institute, Inc., Redlands, CA). Week numbers used to indicate the timing of ice retreat were defined using the International

Organization for Standardization (ISO 8601:2000 (E)) week numbering system (ISO, 2000). This was not the same week numbering system used by Wyllie-Echeverria (1996; pers. comm.), so the Wyllie-Echeverria retreat data set was converted prior to comparison.

The calculated southernmost extent in the data set and that of Wyllie-Echeverria (1996) were slightly different for some years, most likely due to minor differences in source maps. However, major discrepancies were found in the timing of ice retreat. The definition of ice retreat used by Wyllie-Echeverria (1995) does not address re-advances of the ice sheet. Re-advances of the ice sheet occurred multiple times during the time period making the previous definition problematic in its usage. For this reason, the timing of retreat was redefined as sea ice removal from the middle shelf (59.00°N) with no subsequent extended (>1 week) returns of ice to the middle shelf, and the index recalculated. While the two estimates of retreat were significantly correlated ($r = 0.75$, $p < 0.001$, $n = 19$), this new definition provided a more definitive estimate of ice retreat along 169°W.

Because recent work focused on ice dynamics at the M2 mooring (Fig. 1) (Stabeno et al., 1998, Hunt et al., 2002), the southern extent and timing of retreat was calculated for the meridian 164°W. Indices calculated along both 164° and 169°W were significantly correlated with one another for both maximum sea ice extent ($r = 0.57$, $p = 0.011$, $n = 19$) and timing of retreat ($r = 0.70$, $p = 0.002$, $n = 17$). However, as ice did not advance to the middle shelf along 164°W for two of the years in the study period, only those indices associated with 169°W were used for further analyses in order to maximize the degrees of freedom in future comparisons.

While the southernmost extent of sea ice along 169°W provided some information regarding the spatial extent of sea ice, sea ice indices measured along a single transect did not adequately represent the characteristics of ice coverage over a 463,000 km^2 area of ocean. The proportion of the study surface area covered by sea ice was a more relevant index of the pervasiveness of sea ice. Although a time series of the percentage of sea ice covering the larger Bering-Chukchi Seas region was available (Niebauer, 1988), an index

that considered only the NMFS survey area was more appropriate for this study. As the historical maximum ice coverage in the region occurs between February and April (Niebauer et al., 1999) the average weekly percentage of ice-covered ocean was calculated for February, March and April (prior to 1997 only weekly averages were available), from which monthly averages were derived. Monthly averages during this period were thought to provide a good snapshot of yearly ice conditions on the shelf prior to spring melt. Percent ice cover was analyzed using GIS software and calculated as a simple percentage of the survey area containing sea ice. Percentages were cross-validated ($r = 0.97$, $p < 0.001$, $n = 19$) against an updated version of the Niebauer ice anomaly data set (H.J. Niebauer, Univ. Wisconsin, Madison, WI, pers. comm.).

To reduce the number of sea ice variables from the three monthly averages to a manageable and informative set, principal component analysis (PCA) was performed on the monthly sea ice cover averages. Because the three monthly averages were measured on equivalent scales the covariance matrix was used in the PCA to retain the covariance structure of the monthly ice concentrations (Johnson and Wichern, 1999).

The three principal components represent 61.3%, 32.4% and 6.3% of the total variance in the data, respectively. The number of principal components retained for analysis was determined using the broken stick model (Frontier, 1976) based on the percentage of total variance explained by each component. The first two principal components were retained (Table 2). The first component (termed the Spatial Sea Ice Index (SSI)) was a weighted sum of the monthly sea ice concentrations and as such, was proportionate to the average ice cover during the three-month period from February to April. The first principal component was negatively correlated with maximum southern ice-extent along 169°W ($r = -0.46$, $p = 0.046$, $n = 19$) as well as the Niebauer ice anomaly dataset ($r = 0.97$, $p < 0.001$, $n = 19$). The second component (termed the Temporal Sea Ice Index (TSI)) was a comparison between February and April ice concentrations and was negatively correlated ($r = -0.60$, $p = 0.007$, $n = 19$) with the timing of ice retreat along 169°W. Positive TSI values indicated a February-skewed distribution of sea ice concentration and early ice retreat and negative values indicate a April-skewed

distribution with late ice retreat (Fig. 4). The TSI index corresponded well with the timing of phytoplankton blooms (Hunt et al., 2002) predicted by early and late ice retreat (Table 3). PCA of sea ice coverage during February through April reduced the set of sea ice variables to two interpretable variables that provide information on both the spatial and temporal ice coverage over the southeastern Bering Sea shelf.

Water temperature

Both sea surface (SST) and bottom water (BT) temperatures were measured during NMFS summer bottom trawl surveys. The NMFS survey area is divided into six strata. The inner shelf includes strata 1 and 2; the middle shelf, strata 3 and 4; and the outer shelf, strata 5 and 6 (Fig. 3). Temperatures were calculated for the entire survey area as well as for individual shelf regions (inner, middle, outer) and combinations (inner-middle, middle-outer, etc.) using area-weighted averages. Shelf-wide averages were compared to published annual averages (Nebenzahl, 2001). The lowest bottom temperatures were observed over the middle shelf, consistent with the presence of a cold pool. Variability in shelf temperatures decreased towards the outer shelf (Table 4). Shelf-wide average bottom temperature had a significant negative correlation with the SSI index ($r = -0.47$, $p = 0.044$, $n = 19$) and significant positive correlation with the TSI index ($r = 0.62$, $p = 0.004$, $n = 19$) indices. SST was significantly correlated ($r = 0.51$, $p = 0.025$, $n = 19$) with only the TSI index.

The fish species used in this study inhabit different regions of the shelf. Thus, it was not appropriate to use a shelf-wide average to approximate the thermal environment of each species. The most appropriate shelf temperatures for each species were determined from the centers of abundance (centroids) (Gary Walters, NOAA/AFSC, Seattle, WA, pers. comm.) of each the demersal fish species (Fig 3). A 3-4-5-6 strata combination best represented pollock distributions and strata combination 1-2-3-4 was appropriate for the two flatfish species. The regional temperatures were compared to the shelf-wide average using regression analysis (Fig. 5). The slope and intercept of strata combination 1-2-3-4 were significantly ($p < 0.001$, $n = 19$) different from those predicted by shelf-wide

average temperatures, while the slope of strata combination 3-4-5-6 was not different ($p = 0.141$, $n = 19$), but the intercept was ($p < 0.001$, $n = 19$). With the exception of the slope strata combination 3-4-5-6 regional temperatures were significantly different for both pollock and flatfish and were used in further analyses. Regional temperatures better represent the thermal conditions fish experience and the associated interannual variability. SSTs averaged from strata combination 1-3-5 were used to approximate the thermal environment of Pacific herring, because herring inhabit the area from Togiak to Unimak Pass during the summer months (Fig. 3) (Funk, 1990). The slope ($p = 0.008$, $n = 19$) and intercept ($p < 0.001$, $n = 19$) of strata combination 1-3-5 were significantly different than those of shelf-wide average SSTs.

Because groundfish species change their distribution in response to water temperatures (Wyllie-Echeverria and Wooster, 1998) centroid distributions were plotted as a function of annual shelf-wide bottom temperature (Fig. 3). Regardless of water temperature, the abundance centroids (Gary Walters, NOAA/AFSC, Seattle, WA, pers. comm.) of the three species remained in the same shelf regions. Therefore, no corrections were made for interannual changes in temperature-influenced distribution.

Wind stress

Primary production dynamics during the growing season are sensitive to wind-driven mixing in May (Sambrotto et al., 1986) as well as during the summer months (Stabeno et al., 2001). Estimates of annual wind-driven mixing were derived from surface wind speeds obtained from the National Climatic Data Center for St. Paul Island in the Pribilof Island group. North-south and east-west surface wind speeds were converted to a scalar wind speed, which then was used to calculate wind stress using the equation (Knauss, 1997):

$$\tau = 0.002W^2 \qquad (2)$$

where τ = wind stress (N/m^2) and W is scalar wind speed (m/s). Average annual May and average summer (June-July) wind stresses were calculated.

Pelagic prey abundance

Annual estimates of zooplankton biomass (mg/m^3 wet weight) over the eastern Bering Sea shelf for the entire study period were extracted from data collected by the training vessel T/S Oshoro-Maru of Hokkaido University (Faculty of Fisheries, Hokkaido University, 1956-2001). Sampling occurred from June to early August each year using a NORPAC net with 0.33-0.35 mm mesh size, which was towed vertically through the water column from a depth of 150 m (Sugimoto and Tadokoro, 1997). The data set was first filtered to remove sampling stations not within the NMFS trawl survey region. The number of stations within the NMFS survey area ranged from 3 to 51 stations per year, with an average of 18 stations per year. Approximately 50 % of the total sampling occurred over the middle shelf. Data were treated using the same methods outlined in Sugimoto and Tadokoro (1997), where samples that contained salps, jellyfish or large volumes of phytoplankton were excluded from data analyses. Station biomass values were averaged over the study region, yielding annual shelf-wide estimates of zooplankton biomass.

Fish abundance

Estimates of biomass were used as an index of stock abundance for all fish species. Under an assumption of food-limited density dependence, growth is more likely to be influenced by resource partitioning within a particular biomass than by a particular number of fish (Robertson, 1998). Yearly estimates of pollock (Ianelli et al., 2002), yellowfin sole (Wilderbuer and Nichol, 2002) and rock sole (Wilderbuer and Walters, 2002) abundance were extracted from North Pacific Fisheries Management Council (NPFMC) stock assessment and fisheries evaluation (SAFE) reports. Given the predominance of cannibalism in the southeastern Bering Sea pollock population (Table 1), estimates of age-0 pollock were used as an additional proxy of prey availability. These

data were obtained by using the number of NMFS-estimated age-1 pollock in the year t+1 (Ianelli et al., 2002). Because of the dietary overlap of rock sole and yellowfin sole (Lang et al., 1995) and as these two flatfishes comprise over 50% of the benthic infauna consumers in the Bering Sea (Livingston et al., 1999), inter- and intra-species density-dependence was analyzed. Biomass estimates of Pacific herring were based on aerial surveys of spawning aggregations and in-season catch data (ADF&G, 2001).

Statistical analysis

Statistical procedures were performed using SAS statistical software (SAS Institute Inc., 1999). Analysis of variance (ANOVA) was utilized in assessing sexual and regional growth differences of the fish species. Correlation analysis was used in the variable screening process, testing the inverse growth hypothesis, mean length-at-age analysis and condition factor analyses. In all analyses results were considered statistically significant at $p < 0.05$.

Growth analyses were restricted to those relationships outlined in the conceptual model (Fig. 2) and test the two primary hypotheses. Stepwise linear regression analyses were used to select candidate growth models for each age/species combination as well for the average species growth response. An automated stepwise process was used because of the large number of possible models. Prior to conducting analyses, assumptions of normality and variable independence were checked. Collinearity among explanatory variables was assessed prior to model selection by calculation of variance inflation factors (VIF). All VIF values were < 10 indicating that collinearity among the independent variables was not a serious problem (Neter et al., 1996). Stepwise regression was performed using inclusion and exclusion levels set at $p < 0.05$. Model fit was assessed through examination of residual plots. Studentized residuals exceeding ± 2 were considered outliers (Neter et al., 1996).

Based on data availability and results of variable screening steps the variables entered into the species-specific stepwise selection models were:

Pollock (WP): G_{WP}: SSI, TSI, W_{May}, W_{Summer}, $BT_{2,3,4,5}$, Z, $P_{age\text{-}0}$, $A_{pollock}$

Herring (PH): G_{PH}: SSI, TSI, W_{May}, W_{Summer}, $SST_{1,3,5}$, Z, $A_{herring}$

Yellowfin Sole (YS): G_{YS}: SSI, TSI, W_{May}, W_{Summer}, $BT_{1,2,3,4}$, Z, A_{yellow}, A_{rock}

Rock Sole (RS): G_{RS}: SSI, TSI, W_{May}, W_{Summer}, $BT_{1,2,3,4}$, Z, A_{rock}, A_{yellow}

Where for each year:

$G_{species}$	Growth of species (mm/year, g/year)
SSI	Spatial sea ice index
TSI	Temporal sea ice index
W_{May}	Average May wind stress (N/m^2)
W_{Summer}	Average summer wind stress (N/m^2)
$BT_{\#,\#,\#,\#}$	Average summer bottom temperature of strata combination (°C)
$SST_{\#,\#,\#}$	Average summer sea surface temperature of strata combination (°C)
Z	Average zooplankton biomass (mg/m^3)
$P_{age\text{-}0}$	Abundance of age-0 pollock (millions)
$A_{species}$	Species biomass (metric tons)

Ice-influenced growth models

Sea ice conditions were central to the conceptual model (Fig. 2). To test the basic assumptions of the conceptual model, that sea ice regulates fish growth by establishing the thermal and prey conditions over the shelf, simple statistical models were created that considered only the influence of sea ice on the average species growth. To accomplish this, the effects that both the spatial and temporal ice indices (SSI and TSI) had on fish growth in a particular year were considered. An average of the SSI and TSI index (A_I index) was calculated and found to provide a single index that divided yearly ice conditions into three basic states (Fig. 6a). The first state ($A_I < -10.7$) was characterized by a strongly negative SSI index and weakly positive-negative TSI index. The one exception occurred in 1985 when both SSI and TSI were negative. The second state ($-10.7 \geq A_I \leq 3.8$) was characterized by slightly positive SSI values and strongly negative

TSI values. The third state ($A_I > 3.8$) was characterized by both positive SSI and TSI values. Based on the interpretation of the TSI and SSI indices, where ice retreat is negatively correlated with the TSI index and water temperature was positively correlated with the TSI index and negatively with the SSI index, the first state was typified by warmer temperatures and average timing of sea ice retreat. Cold temperatures and a late sea ice retreat were observed in the second state and average temperatures and earlier sea ice retreat characterized the third state. The state characteristics, as defined by the A_I index were supported by direct observations of shelf temperatures and timing of ice retreat (Table 5). Based on the growth-control pathways of the conceptual model, parabolic growth responses to the A_I index were predicted (Fig. 6b). Simple polynomial growth models were constructed for all four species using the A_I index as the explanatory variable to test the theorized response. The ice-influenced models had the basic form of:

$$G_{sp} = \alpha + \beta_1 A_I + \beta_2 A_I^2 \quad (3)$$

where G_{sp} was the average growth, A_I was the SSI-TSI average, α was the intercept and β_1 and β_2 were scaling parameters. No transformations of the A_I variables were needed to correct for collinearity between the first and second-order terms as both variables were already centered (mean approximately 0) (Neter et al., 1996).

Average growth comparisons

To test the hypothesis that pelagic and benthic feeders exhibit an inverse growth response under food-mediated growth, the correlations between the average standardized growth responses of all species were calculated. Herring weight was used because growth was much larger relative to size-at-age using growth in weight than using growth in length (Table 6). Growth differences were more detectable using growth in weight.

Mean length-at-age

Mean length-at-age (MLA) is a repository of yearly growth information, interfering with the detection of interannual environmental influences of growth. For instance, strong

density-dependent growth in a juvenile cohort may be retained in the length-at-age signal for many years, interfering with subsequent interannual growth signals. Additionally, the occurrence of compensatory growth following years of depressed growth (Ali et al., 2003) may obscure environmental induced changes in annual growth as observed in MLAs. However, comparative examination of MLA among young age classes of different species and guilds could provide insight into early life history growth response (Walters and Wilderbuer, 2000). Because of the noted problems with MLA, the examination was limited to the youngest age classes for which a complete time series was available. These age classes were: age-2 pollock; age-4 herring; age-3 yellowfin sole; and age-3 rock sole. To overcome differences in scale, annual MLA data were converted to anomalies by subtracting the period average. The anomalies werew then compared using correlation analyses as well as by descriptive analysis of yearly trends.

Condition factor

To determine if pre-summer fish condition affects subsequent growth, the relationship of condition factor to growth was assessed. Adult pollock are known to maintain constant condition factors at maintenance rations (Yoshida and Sakurai, 1984), which suggests weight is maintained at the expense of length-growth when food availability is low. Given this, it was hypothesized that fish with a higher pre-summer condition factor would be more likely to grow faster. Also, because feeding may have occurred prior to the survey, the relationship between condition factor and those growth control variables selected by stepwise regression was assessed.

Condition factors were calculated as Fulton condition factors (K) using the relationship:

$$K = (W/L^3) \times 10^5 \qquad (4)$$

where K is the condition factor (kg/m), W is the weight (g) and L is the length (mm).

A yearly average condition factor was calculated separately for males and females. Individual weight-at-age data were obtained from the same sources as mean length-at-age data. Annual condition factors for each sex were calculated as the average of all age classes (n>300 in all cases). Sufficient (≥ 3 years) annual length and weight data to perform correlation analysis on condition factors were available for pollock, yellowfin sole and herring, but not rock sole. The relationship between yellowfin sole growth controls and condition factors could not be assessed because of insufficient degrees of freedom. The yellowfin sole growth model contained two variables and only three years of length-weight data existed to determine condition factors.

Recruitment

The growth rate of juvenile fish can influence recruitment to the adult spawning populations (van der Veer et al., 1994). Elevated growth in the juvenile stage can positively affect overwintering survival, prey capture and predator avoidance (Paul and Paul, 1999). While the size and species of prey consumed varies, there is considerable overlap in the basic prey items (pelagic prey, benthic prey) of juvenile pollock (Grover, 1991) and yellowfin sole (Holladay and Norcross, 1995) with that of adults (Table 1). Therefore, conditions favorable for adult growth may also be favorable for juvenile growth and recruitment. Increased recruitment of juvenile pollock to the adult population (≥ age 2) has been shown to be related to environmental variables such as air temperature and ice cover (Quinn and Niebauer, 1995), though specific mechanisms are unclear. To test whether these relationships could be caused by growth variability the relationship between recruitment and growth was assessed for walleye pollock and yellowfin sole.

Recruitment was defined as the number of age-2 fish in the study area. Estimates of the number of age-2 fish were obtained from NPFMC SAFE reports for pollock (Ianelli et al., 2002) and yellowfin sole (Wilderbuer and Nichol, 2002) for the years 1983 to 2002. To account for density-dependent effects on recruitment, a Ricker spawner-recruit curve was fit to the recruitment data using estimates of spawner biomass for the years 1981 to 2000 obtained from the same sources as the recruitment estimates (Fig. 7). The

curve fits were significant for both pollock ($p = 0.010$, $n = 20$) and yellowfin sole ($p = 0.033$, $n = 20$). The residuals from the curve were used as corrected estimates of recruitment in all further recruitment-growth analyses. There were no direct measurements of juvenile growth so standardized adult growth was used as a proxy for growth conditions experienced during the juvenile stages. As recruitment was defined as number of age-2 fish, growth could have influenced survival at age-0 or age-1. Cross-correlations were performed between recruitment and standardized adult growth with the recruitment time series lagged accordingly to approximate the growth conditions during age-0 and age-1 life stages. In addition, the recruitment time series of the two species were compared using correlation analysis to determine if conditions which produce strong year classes of pelagic and benthic feeders can occur during the same year.

Results

Sexual and regional differences

ANOVA results indicate sexual and regional growth differences did not need to be considered in the growth models. The only significant regional/sexual differences detected in pollock were regional effects in age-2 ($F_{3, 71} = 3.98$, $p = 0.049$) and age-4 fish ($F_{3, 72} = 4.52$, $p = 0.037$). Among herring, yellowfin and rock sole, only age-7 ($F_{1, 34} = 4.79$, $p = 0.036$) and age-8 ($F_{1, 34} = 8.39$, $p = 0.007$) rock sole exhibited significantly different growth responses between sexes. Because of the lack of widespread sex and regional effects among the growth response of all species, further analysis did not consider sex and regional populations separately. All species were treated as single-sex, homogenous populations.

Stepwise growth models

The stepwise analyses were primarily used to describe the growth control factors for the species rather than particular age classes. Models were developed for all age classes to ensure that significant variables selected for the age-averaged models were not spurious.

The resulting age-specific models are used only to support the age-averaged models, which will be discussed in more detail. In general the explanatory power of all models decreased with age, the age-averaged models explained the greatest amount of variability in the case of pollock and yellowfin sole.

Pollock growth models contained only two variables of significance: age-0 pollock abundance and TSI index (Table 7). The age-averaged growth model,

$$G_{WP} = -0.0001 + 0.0278TSI \quad (5)$$

contained only TSI as an explanatory variable and accounted for 50 % of the variability in age-averaged annual growth. In addition, the age-averaged model successfully forecasted above/below average growth with a 68% success rate, and the direction of change of growth from one year to the next with a 72% success rate (Fig. 8). Studentized residuals indicated that there were no outliers in the data set. The TSI index was persistent from ages 6 through 8, after first appearing in the age-4 class, with the explanatory power decreasing with age.

No significant age-averaged growth model could be produced for Pacific herring. Stepwise selection on both length and weight growth indices selected only surface temperature in age-4 fish as a significant variable (Table 7), explaining 46% and 33% of growth variability in length and weight respectively. This type of positive relationship would be expected under temperature-controlled growth.

Stepwise selection methods for yellowfin sole selected three different explanatory variables: May wind stress, zooplankton, and yellowfin sole abundance (Table 7). The age-averaged model,

$$G_{YS} = 2.7823 - 17.2017W_{May} - 0.0018Z \quad (6)$$

explained 61% of the growth variability in the age-averaged annual growth increments. In addition, the model successfully forecast above/below average growth 89% of the time

and the direction in change of growth form one year to the next with a 82% success rate (Fig. 8). No outliers were evident in the Studentized residuals. Yellowfin sole abundance showed a positive relationship to growth in age-6 fish, though since it occurred in only one age-class, its contribution to growth of the species as a whole was limited.

Rock sole stepwise selection selected five different explanatory variables: zooplankton abundance, yellowfin sole abundance, bottom temperature, summer wind stress, and SSI (Table 7). Only bottom temperature appeared in multiple age classes as well as the age-averaged model. In the age-averaged model,

$$G_{RS} = 1.0665 - 0.4634BT_{1,2,3,4} \quad (7)$$

bottom temperature explained 26% of the growth variability. The model accuracy in forecasting above/below average growth was 78%, and 82% accuracy in forecasting the direction in change of growth from one year to the next (Fig. 8). The 1984 data point was identified as an outlier. Re-running the model with 1984 removed improved model fit ($r^2 = 0.32$) and significance ($p = 0.019$, $n = 17$).

Ice-influenced growth models

The A_I ice-influenced models were significant for only one species. The A_I index explained a significant ($p = 0.022$) amount of the variability in pollock growth over the study period. Both herring length and weight models were not significant ($p = 0.924$ and $p = 0.498$, respectively). The models for the two benthic feeders, yellowfin sole ($p = 0.198$) and rock sole ($p = 0.259$), also were not significant. Studentized residuals showed 1984 to again be an outlier in the rock sole model fit. Removal of this year improved the model fit ($r^2 = 0.24$) but was still not significant ($p = 0.141$, $n = 17$). The model equations for all species are as follows:

$$G_{WP} = -0.2414 + 0.0257A_I + 0.0013A_I^2 \quad (8)$$

$$G_{PH(l)} = -0.0643 - 0.0032A_I + 0.0003A_I^2 \quad (9)$$

$$G_{PH(w)} = 0.0794 + 0.0169A_I - 0.0004A_I^2 \quad (10)$$

$$G_{YS} = 0.2953 + 0.0049A_I - 0.0015A_I^2 \quad (11)$$

$$G_{RS} = 0.3122 + 0.0095A_I - 0.0016A_I^2 \quad (12)$$

The conceptual model predicted (Fig. 6) that the ice-influenced model fits would be concave (positive second-order term) and have a positive intercept for pelagic feeders. For benthic feeders the model predicted a convex fit (negative second-order term) and negative intercept. The model fits for pollock, yellowfin and rock sole fit the data as predicted by the conceptual model (Fig. 9). The model fits of Pacific herring were too poor to allow interpretation of the nature of the curve.

Average growth comparisons

Correlation analysis of the average growth responses of the four species showed some evidence of uniform guild growth responses (Table 8). A statistically significant relationship existed between the growth of the two pelagic species, pollock and herring, when herring weight growth was used (Fig. 10a). There was no significant relationship when comparing pollock growth to herring length growth. Interestingly, both yellowfin sole and rock sole had unexpectedly high correlations, though not statistically significant, with Pacific herring. The two benthic feeders, yellowfin sole and rock sole, exhibited no significant relationship with each other. Despite the lack of a significant relationship, a plot of the annual standardized growth showed similar trends (Fig. 10b), with the exception of the period from 1982 to 1984. Removal of these years from the analysis improved the correlation coefficient, though the relationship was still not significant ($r = 0.51$, $p = 0.052$, $n = 15$).

Mean length-at-age

A general inverse trend was observed between pollock and yellowfin sole. Age-2 pollock and age-4 Pacific herring mean length-at-age (MLA) anomalies are negatively related, though not significantly ($r = -0.32$, $p = 0.19$, $n = 19$). Age-3 yellowfin and age-3

rock sole MLA anomalies were uncorrelated ($r = 0.10$, $p = 0.70$, $n = 19$). Despite the lack of significance between walleye pollock and yellowfin sole MLA, the data do tend vary inversely (Fig. 11a), in support of the inverse growth hypothesis. However, the correlation was not significant ($r = -0.32$, $p = 0.19$, $n = 19$). The only significant relationship among species MLA was between herring and yellowfin sole ($r = 0.56$, $p = 0.012$, $n = 19$). The variability of the herring MLA time series undergoes low-frequency fluctuations in growth (Fig. 11b), while the MLA anomalies shown by pollock, yellowfin sole and rock sole fluctuate from positive to negative at much higher frequencies.

Condition factor

There was evidence of condition factor affecting the subsequent growth of pelagic consumers. The relationship between condition factor and subsequent pollock growth was significant for males ($r = 1.00$, $p = 0.002$, $n = 3$), but not for females ($r = 0.99$, $p = 0.077$, $n = 3$) (Fig. 12a). The TSI index was related to male and female growth, with a significant relationship for males ($r = 1.00$, $p = 0.023$, $n = 3$), but not females ($r = 0.99$, $p = 0.064$, $n = 3$) (Fig. 13). The sample sizes of these analyses were extremely small due to limited availability of condition factor data. The growth of herring, measured as length, was related to the condition factor of both male ($r = 0.49$, $p = 0.020$, $n = 19$) and female ($r = 0.46$, $p = 0.026$, $n = 19$) herring (Fig. 12b). No relationship was observed when weight was used as the growth index (males: $r = 0.09$, $p = 0.685$, $n = 19$; females: $r = 0.04$, $p = 0.886$, $n = 19$). Yellowfin sole showed no significant correlations (males: $r = 0.42$, $p = 0.727$, $n = 3$; females: $r = 0.54$, $p = 0.636$, $n = 3$) between pre-summer condition and subsequent seasonal growth, though these analyses, like those for pollock, were restricted by small sample size.

Recruitment

Results of the cross-correlations between pollock and yellowfin sole recruitment and adult growth are shown in Table 9. None of the relationships were significant at the $p = 0.05$ level. Plots of the data show the weak relationship between pollock recruitment and

growth conditions (as estimated by standardized adult growth) during age-0 and age-1 life stages (Fig. 14a). While correlations between yellowfin sole growth conditions during age-0 and recruitment residuals were not significant (Table 9), there is a noticeable trend for yellowfin sole recruitment to be improved when above average growth conditions occur during the age-0 life stage (Fig. 14b). A similar relationship is not evident between recruitment and growth conditions during the age-1 stage (Fig. 14b). The recruitment residuals of pollock and yellowfin sole exhibited a significant ($p = 0.023$, $n = 20$) positive relationship, with strong year classes of pollock and yellowfin sole occurring during the same years (Fig. 15).

Discussion

Food availability is the predominant growth-control pathway for southeastern Bering Sea fish species. Stepwise models show that for walleye pollock and yellowfin sole, factors affecting the amount of benthic-pelagic coupling, and subsequent fate of primary production, are important in explaining interannual variation in the growth of both pelagic and benthic feeding species. These finding support the ice-controlled switch of pelagic-benthic production shown in the conceptual model (Fig. 2) and first proposed by Walsh and McRoy (1986). This inverse production signal is also evident in the MLA record of walleye pollock and yellowfin sole, as well as the fits of the ice-growth models (Fig. 9), though such a relationship is not observed in the growth rates of these two species.

Food mediation of growth is supported by laboratory studies on both pelagic and benthic feeders. Experiments with walleye pollock showed food to have a greater effect than temperature on growth regulation (Yoshida and Sakurai, 1984). Over a 7° C temperature range (3° to 10° C) yellowfin sole showed no significant changes in the slope of the consumption to growth relationship (Smith et al., 1991), further supporting the relative importance of food availability in mediating growth. The rock sole stepwise model of this study shows a negative relationship of growth to bottom temperature,

seemingly contradicting a food-mediated growth mechanism. However, while cold temperatures may inhibit growth rates (Smith et al., 1986) such inhibition is countered by the increased benthic food availability associated with colder temperatures (Fig. 6, AI state 2), such that benthic growth conditions are enhanced when ice cover is heavy and ice retreat occurs late in the spring.

The conceptual model predicts a positive relationship among the growth rates of different species if temperature is the primary control of growth. The positive relationship among the growth rates of the four study species (Table 8) could represent a temperature influence on growth, though if temperature were important in controlling growth it should have been a significant variable in the stepwise models. Detection of temperature influences may be problematic in this study due to the narrow range of temperatures observed over the Bering Sea shelf (Brander, 1994). A single stock growth analysis of north Atlantic groundfish (Ross and Nelson, 1992) had an observed temperature range (7.47°C to 12.50°C), comparable to the 3° C range in average shelf bottom temperature observed in this study (0.83°C to 3.43°C), and no detectable influence of temperature was found. Conversely, in a large regional inter-stock comparative study on Atlantic cod, temperatures ranged from 2°C to 11°C and explained 95 % of the growth variability among stocks (Brander, 1995). Thus temperature effects may only be detectable when fish species are subjected to a wide range of temperatures.

Based on the ice-growth and stepwise model results for pollock, the three sea ice indices developed appear to provide ecologically useful and interpretable information. An interesting feature of the TSI index is that large TSI values, corresponding to maximum pollock growth (Eq. 5), occur when February ice coverage is extensive and ice retreats from the shelf early (Fig. 4). This implies that maximum pelagic production is not only dependent on an early retreat, but also on some degree of winter ice coverage. Ice-cover, by promoting under-ice production and ice-edge production, increases the total overall primary production of the Bering Sea (McRoy and Goering, 1974). However, the significance of February ice coverage is unclear. Given the low light levels and low under-ice primary production measured in February (McRoy and Goering, 1974) it is

doubtful that winter ice cover has much direct influence on total annual production. It is more likely that winter ice cover is important because the greater the ice cover prior to the spring retreat, the greater the area of the shelf that will receive ice-associated production inputs from sizeable under-ice spring blooms that can occur in early spring (Stabeno et al., 1995).

While pollock and herring show a high degree of correlation among growth rates, the inability to generate significant stepwise growth models for herring, and the low explanatory power of the ice-growth models for herring imply that herring is not strongly influenced by shelf dynamics. After spawning in northern Bristol Bay the stock migrates to summer feeding grounds near Unimak Pass (Fig. 3) (Funk, 1990). The oceanography of the Aleutian passes, including both production dynamics and thermal environment, is very different from that of the shelf environment (Stabeno et al., 1999), and the conceptual model for the southeast shelf may not apply to the Togiak herring stock. Based on the ecology of the two species, pollock is a better representative of the pelagic feeder response to shelf conditions and the pathways shown in the conceptual model.

Both yellowfin and rock sole are benthic infauna consumers inhabiting similar habitats (McConnaughey and Smith 2000) in approximately the same region of the Bering Sea (Fig. 3). It was predicted that, given the similarity in ecological niches, they would exhibit a similar growth response to environmental conditions. Growth models provided better fits of the yellowfin sole data, and it could be that like pollock, yellowfin sole better represent the benthic feeder growth response. Yellowfin sole have a broader diet than rock sole (Lang et al., 1995), with no prey-type (Table 1) comprising more than 25% of the diet by weight, while rock sole feed predominantly on marine worms (>60%). While stock biomass does not appear in the age-average model results of either species, the MLA of rock sole decreased in the 1980's during a period of increasing stock size (Walters and Wilderbuer, 2000), suggestive of a density-dependence growth response by rock sole. Because of a broad prey base and possibility of density-dependent effects on rock sole growth, yellowfin sole probably better represents the general growth response of benthic consumers.

Results presented here show that the growth of both pelagic and benthic feeders is related to changes in the physical environment. Therefore, large-scale perturbations, such as regime shifts, have the potential to drastically affect fish growth rates. If the finding that there is a negative relationship between pollock growth and timing of ice retreat is extrapolated back to the regime prior to 1976/77, it is likely that pollock growth would be less than that observed from 1982 to 2000 (Fig. 16). Observations of mean length-at-age from the central Bering Sea support this conclusion of slower growth pre-1977 (Akira et al., 2001). The strong relationship between pollock growth and timing of ice retreat may be due to the fact that both pelagic food availability and temperature are positively related to the TSI index (negatively to the week of ice retreat). Because both food and temperature would be affected in similar ways by large-scale climatic changes, the resultant growth response of pelagic feeders to large-scale changes may be amplified. Increased size of the cold pool during years of greater ice coverage could cause a greater overlap of juvenile and adult pollock, leading to increased cannibalism (Wyllie-Echeverria and Wooster, 1998). Such an occurrence might offset otherwise poor growth conditions for pollock during cold years. The relationship between benthic feeders and ice-retreat is not as clear. However, unlike the situation for pelagic feeders, high benthic food-availability and a favorable thermal environment do not co-occur (Fig. 6). This likely explains why clear relationships are not observed between benthic-feeder growths and the timing of ice retreat. Such an inverse relationship between food and temperature may also act to buffer the benthic-feeder growth response to large-scale climatic changes, provided warmer temperatures do not cause the metabolic demands to exceed food-availability.

Fish growth is positively related to the condition factor of pelagic fish (Fig. 12), both in this study in the southeastern Bering Sea and in pollock from the western Bering Sea (Balykin and Buslov, 2002). A relationship between growth in length and condition factor was not evident in yellowfin sole. However, yellowfin sole are known to preferentially allocate energy to growth in length as opposed to weight when food is limited (Paul et al., 1995). The relationship between growth in length and condition factor

is more direct in pollock, as they maintain weight at the expense of growth in length when food availability is low (Yoshida and Sakurai, 1984). Therefore, growth in pollock length is more likely when condition factors are high. The relationship of pollock condition factors to the TSI index suggests that growth, primarily growth in weight, is occurring prior to the start of the survey or that pollock exit the winter with a higher condition factor when winters are less severe. Regardless, during years of elevated growth rates, pelagic fish are likely to have a greater weight to length ratio and represent a more nutritionally energetic prey for potential predators. While the relationship between condition factor and energy content is weak for Pacific herring (Paul et al., 2001), a direct relationship of both length (Ciannelli et al., 2002) and condition factor (Harris, 1985) to energy content has been shown for larval and juvenile pollock, though this remains untested for adult pollock. Given this relationship, fish growth may provide a useful way of retrospectively assessing the nutritional value of marine bird and mammal prey.

While this study deals only with growth of adult fish, the potential importance of benthic-pelagic coupling on the growth and subsequent recruitment of juvenile fish is important to consider (Townsend and Cammen, 1988). Age-0 pollock have a survival strategy of rapid length growth in the first year, which is theorized to increase swimming speed and facilitate prey capture and predator avoidance (Paul and Paul, 1999); therefore changing growth rates should influence pollock recruitment . Increased growth of juvenile flatfish has also shown to have a positive effect on recruitment (van der Veer et al., 1994). The results of this study suggest that for pollock, growth conditions in the juvenile stage are not a major determinant of recruitment strength. While there was a trend for greater yellowfin sole recruitment when growth conditions were above average (Fig. 14b), it is premature to conclude that this is evidence of a growth influence. If recruitment is influenced by growth during the age-1 life stage, and this growth is driven by food-availability, an inverse relationship in the recruitment patterns would be expected under the conceptual model. This does not appear to be a plausible mechanism to explain recruitment patterns based on the comparison of pollock and yellowfin sole recruitment patterns (Fig. 15). Because growth of juveniles was not directly measured for these

analyses, but rather inferred from the growth response of the older age classes, it is impossible to determine if juvenile growth was accurately estimated. A more thorough analysis of the pollock-yellowfin sole recruitment relationship and the possible driving mechanisms is warranted, as well as a re-analysis of the growth-recruitment relationship using more accurate estimates of juvenile growth.

This study made critical assumptions and simplifications that undoubtedly affect the results. These assumptions and simplifications can be divided into two categories: those directly related to fish growth and those related to the production dynamics of the southeastern Bering Sea. An important fish growth assumption was that the bulk of growth occurred after survey collection, which is probably correct (Maeda, 1972; Paul et al., 1993; Fritz Funk, ADF&G, Juneau, AK, pers. comm.). However, it is unknown how much growth actually occurs prior to the survey and how it varies interannually in response to a changing environment. This study also assumed that all energy surpluses are used for somatic growth. However, surplus energy can also be used for reproduction (Calow, 1985). The amount and variability of energy allocated for reproduction depends on the energy surplus available and the energy allocation strategy of the particular species (Ware, 1984). Reproductive effort was not considered in these analyses because of the paucity of information available on the energy allocation strategies of the study species. The occurrence of compensatory, or catch-up, growth in some fish species also has the ability to alter the effects that environmental influences have on annual growth rates (Ali et al., 2003). In yellowfin sole, there is limited capacity for compensatory growth (Paul et al., 1995), but the capacity of the other three study species is unknown. This study sought to determine the habitat restraints to growth, a step that must be taken prior to detection of compensatory growth in natural populations (Ali et al., 2003).

Shelf production dynamics were simplified to assess basic growth response to changes in ice conditions. While only vertical mixing was accounted for in the conceptual model, horizontal advection is also important in controlling nutrient availability to the mixed layer (Stabeno et al., 1998), though annual estimates of horizontal advection dating back to 1982 do not exist. The model also assumed that ice-edge initiated and late

spring blooms were mutually exclusive, though it is known that both ice-edge and open water blooms can occur in the same year (Hunt et al., 2002). Blooms of both types are also not of equal magnitude from year-to-year (Hunt et al., 2002), nor are they of the same quality, as evidenced by the by the large coccolithophorid bloom that occurred in the eastern Bering Sea in 1997 and to some degree in 1998 (Napp and Hunt, 2001). The coccolithophorid blooms did not appear to impact the abundance of many zooplankton species (Stockwell et al., 2001) or the subsequent growth of pelagic species (Fig. 7), though the growth of both benthic feeders was below average during these years, with 1998 being the worst growth year of the study period (Fig. 7). The bloom could have decreased the quality of detrital matter reaching the benthos during these years, further inhibiting the growth of benthic feeders during these warm years.

Another simplification in regards to Bering Sea production was that prey abundance was assumed to have an even spatial distribution and to be independent of the prior-year abundance. The southern limit of ice extent is highly variable, not only interannually, but also spatially (Niebauer et al., 1999). The spatial variability is certainly capable of influencing local bloom dynamics, which could lead to patchy production in both the pelagic and benthic environments. However, as the range of these species over the shelf is quite broad, it is unclear what effects localized production would have on the overall interannual growth of the species. Also, as prey species have life spans greater than one year, it is likely that prey abundance from year to year is not independent. Model fits may improve by correcting for variable autocorrelation (Krohn et al., 1997) in future studies. Annual pelagic prey availability was also assumed to be affected only by intraspecific competition. However, consideration of interspecific competitors by including other pelagic planktivores, such as Pacific salmon, forage fish and jellyfish, may yield more information regarding pelagic food availability.

Despute the shortcomings of the approach, by investigating the relationships among growth of pelagic and benthic feeding fish as well as the environmental controls of the individual fish species, the conceptual model and associated analyses provide a general framework from which to launch hypothesis-driven observational studies and more

complicated retrospective statistical studies. The connections described reflect the current production paradigm for the southeastern Bering Sea, but many of these relationships, such as the association between timing of ice retreat and benthic invertebrate production, remain untested. In addition, the data sets used, especially the estimates of pelagic prey, are limited by sample size and spatial and temporal coverage. Without better estimates of intermediate secondary production the mechanisms of the relationship between ice retreat and fish growth remains tenuous. Also, while correlation analyses like those performed in this study are useful in determining important relationships, they do not identify the specific physiological mechanisms directly responsible for differential growth. Bioenergetic modeling can provide this mechanistic information (Krohn et al., 1997) and should be considered as a next step. However, the conclusion of this study, that relationships between the environment and fish growth do exist, is a necessary and important first step to understanding the growth controls of southeast Bering Sea fish species.

Conclusions

Previous research regarding the influence of sea ice on the productivity of the Bering Sea has suggested that sea ice has the ability to influence higher trophic levels by controlling the timing and the subsequent fate of primary production. This research utilized the current knowledge of the Bering Sea ecosystem to construct a conceptual model which successfully explains the response of pelagic and benthic growth to annual ice conditions. The food pathways of the conceptual model were most important in influencing growth of walleye pollock and yellowfin sole. Mean length-at-ages of these two species showed evidence of the inverse growth, which was predicted by the food-control pathway of the conceptual model. Temperature was found to be significant in explaining rock sole growth. However, the negative relationship was opposite that predicted by the temperature pathway of the conceptual model. The ice-influenced growth models explain this finding by considering the relationship between the temperature and food supply of benthic consumers, and suggest that this may also be a response to food availability. The ice-growth models further show that pelagic and benthic feeders exhibit inverse growth responses when the influence of food and temperature are considered simultaneously. The relationship between growth and condition factor suggests that growth may be an important proxy in assessing the nutritional quality of marine mammal and seabird diets, especially in regards to walleye pollock. Growth did not appear to influence age-2 recruitment, though direct estimates of juvenile growth are needed before a firm conclusion can be made. The major conclusion of this study is that relationships between the environment and fish growth do exist. This is a finding that is a necessary and important first step to understanding not only the growth controls of southeast Bering Sea fish species, but also energy flow through the ecosystem.

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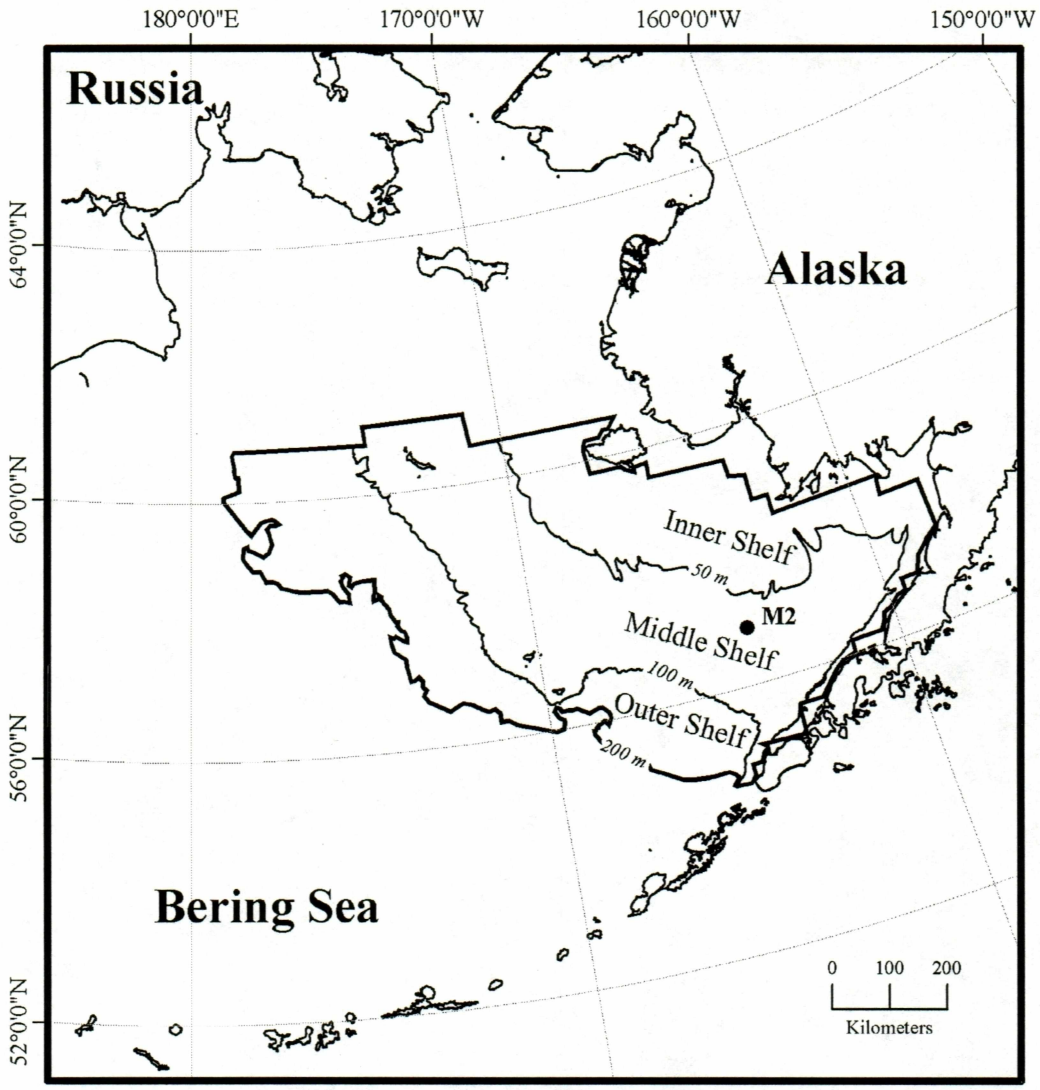

Fig. 1. Map of the southeastern Bering Sea. The NMFS survey area (heavy line), M2 mooring location (56.8° N, 164.0° W) and three hydrographic domains (inner, middle and outer shelves) separated by the 50 m and 100 m isobaths are shown.

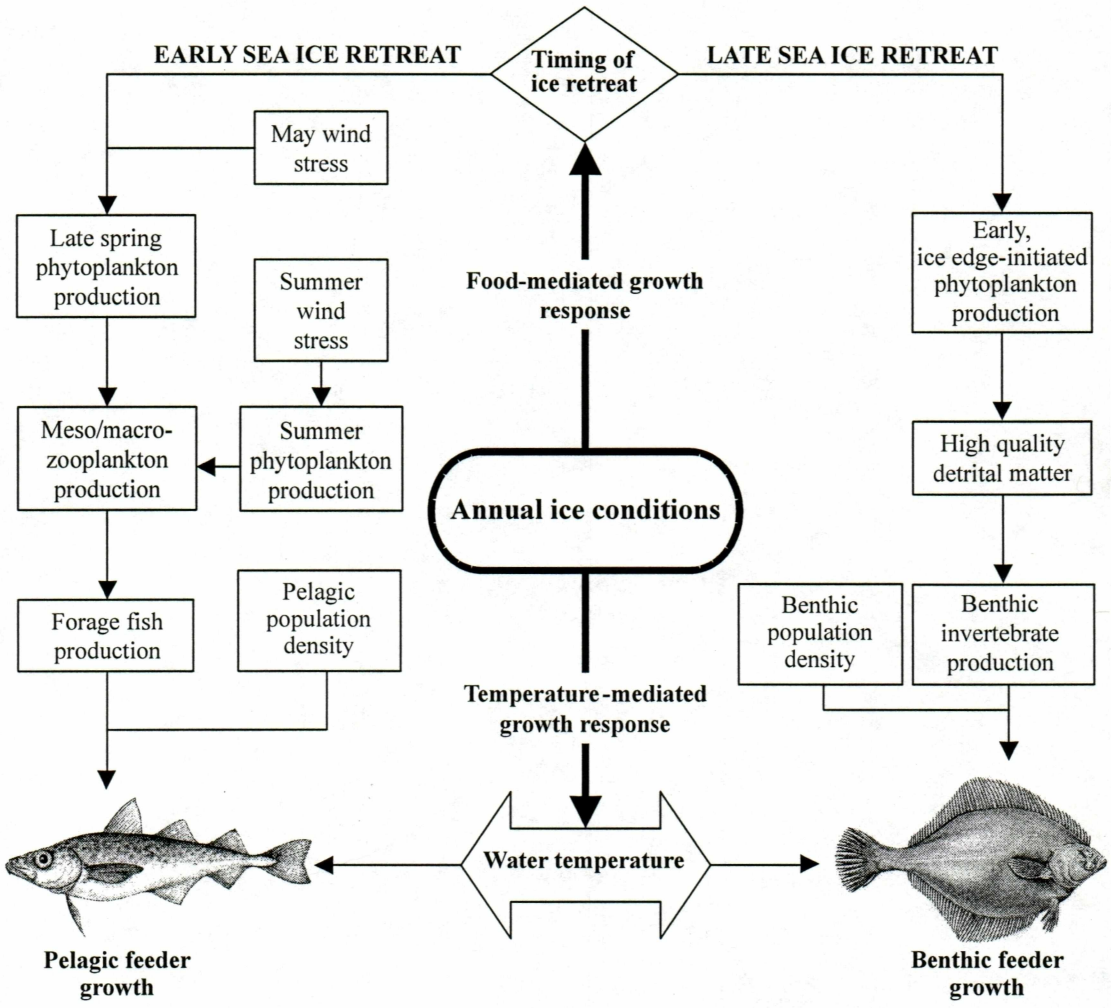

Fig. 2. Conceptual model of hypothesized fish growth control factors over the southeastern Bering Sea shelf. The pathways of the two growth hypotheses, food availability and temperature, are shown. Food availability is tied to phytoplankton-zooplankton coupling and supports growth in either pelagic or benthic feeders dependent on the timing of ice retreat, resulting in an inverse growth response between pelagic and benthic feeders.

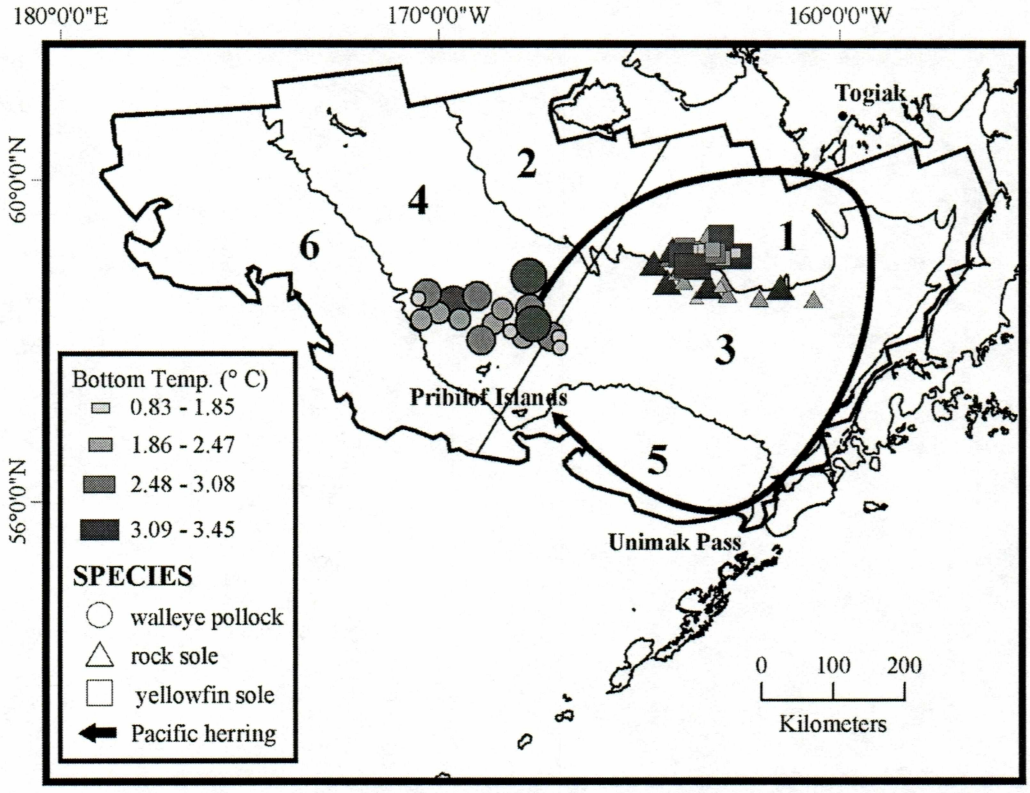

Fig. 3. Annual centers of distributions of the four study species within the NMFS summer bottom trawl survey area for the years 1982-2000. The NMFS survey area is divided into the six survey strata shown. Centroids of groundfish abundance are plotted as a function of annual summer bottom temperature as measured during the NMFS trawl survey. The annual migration pattern of the Togiak herring stock (→) is shown. During the summer months herring inhabit the area between Togiak and Unimak Pass.

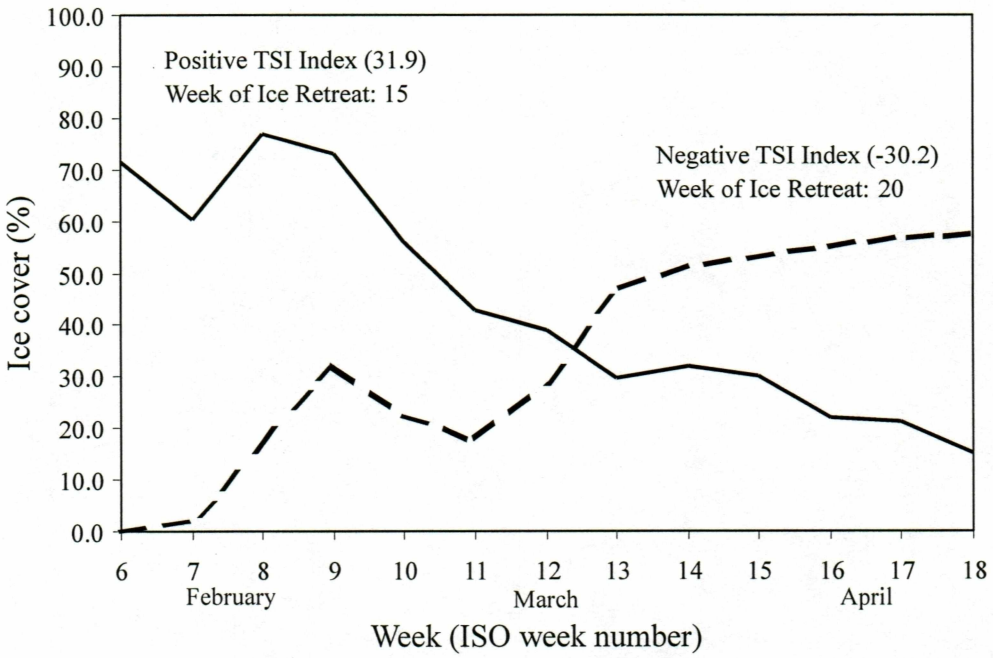

Fig. 4. The percentage of the survey area covered by ice as a function of week number for the two extreme values of the Temporal Sea Ice (TSI) index observed during the study period (1982-2000). Positive TSI values (1998, solid line) indicate early ice retreat and negative values indicate late ice retreat (1985, dashed line). The corresponding timing of ice retreat observed along 169° W is reported for the respective years.

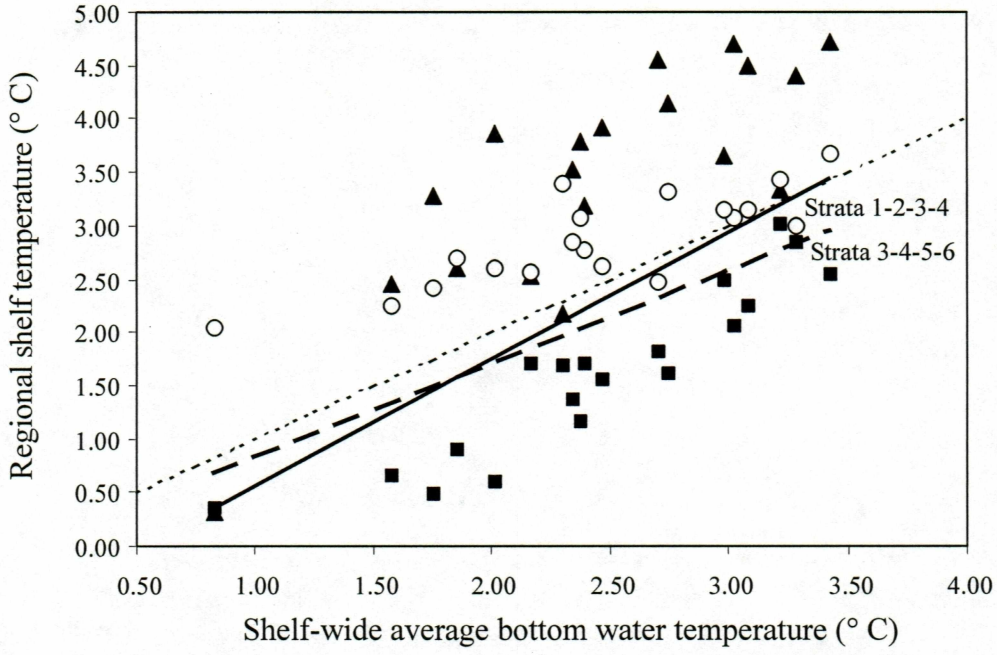

Fig. 5. Annual regional shelf bottom-water temperatures compared to the shelf-wide average for the years 1982-2000. Annual average temperatures of the inner (▲), middle (■) and outer (○) shelves are shown along with regional temperatures of NMFS survey strata combinations 1,2,3,4 and 3,4,5,6. The dotted line represents the 1:1 relationship of regional temperatures to shelf-wide temperatures.

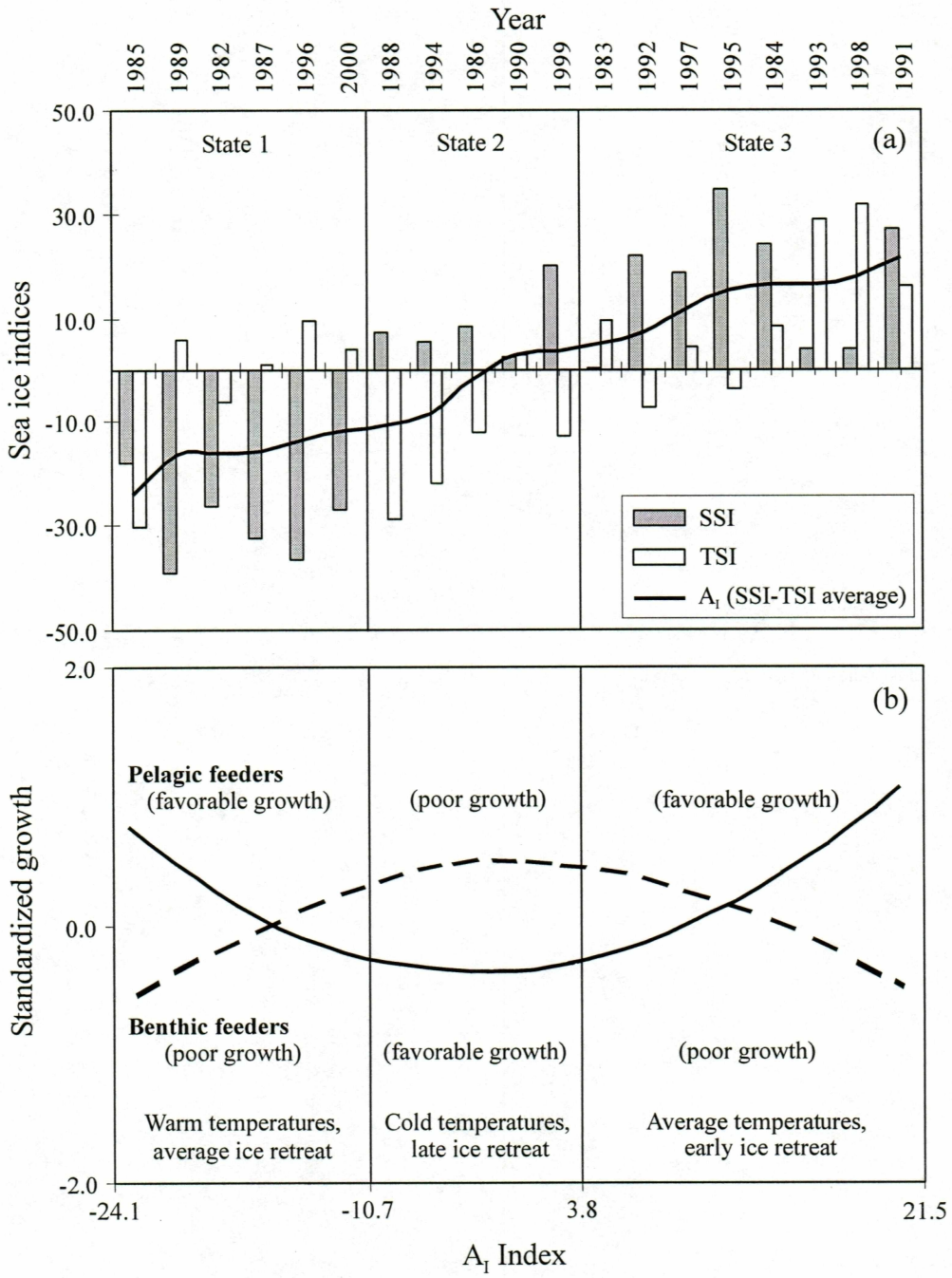

Fig. 6. Conceptual definition of the SSI-TSI Average Ice (A_I) index and implications for fish growth. The A_I index is plotted from lowest value to greatest (a), stippled columns represent SSI values and white columns, TSI values. The lower figure (b) shows the theorized fish growth responses to the A_I index based on the water temperature and food-limited growth mechanisms described by the conceptual model for both pelagic (heavy solid line) and benthic feeders (heavy dashed line).

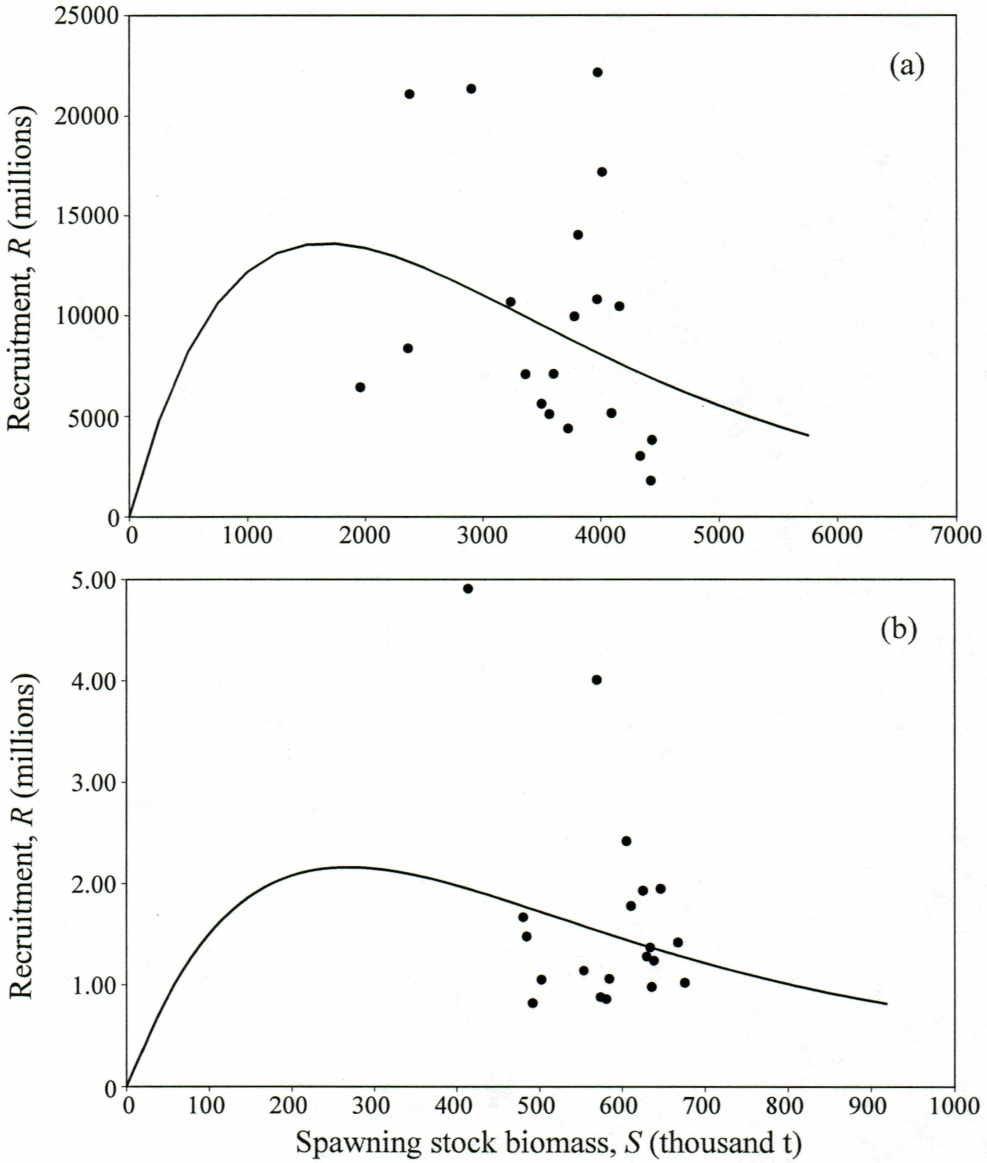

Fig. 7. Relationship between eastern Bering Sea recruitment and spawning stock biomass for walleye pollock (a) and yellowfin sole (b) for the 1981-2000 year classes. Ricker spawner-recruit curves are shown ($R = \alpha S e^{-\beta S}$; pollock, $\alpha = 22315$, $\beta = 6.31 \times 10^{-7}$; yellowfin sole, $\alpha = 20.1$, $\beta = 3.57 \times 10^{-6}$).

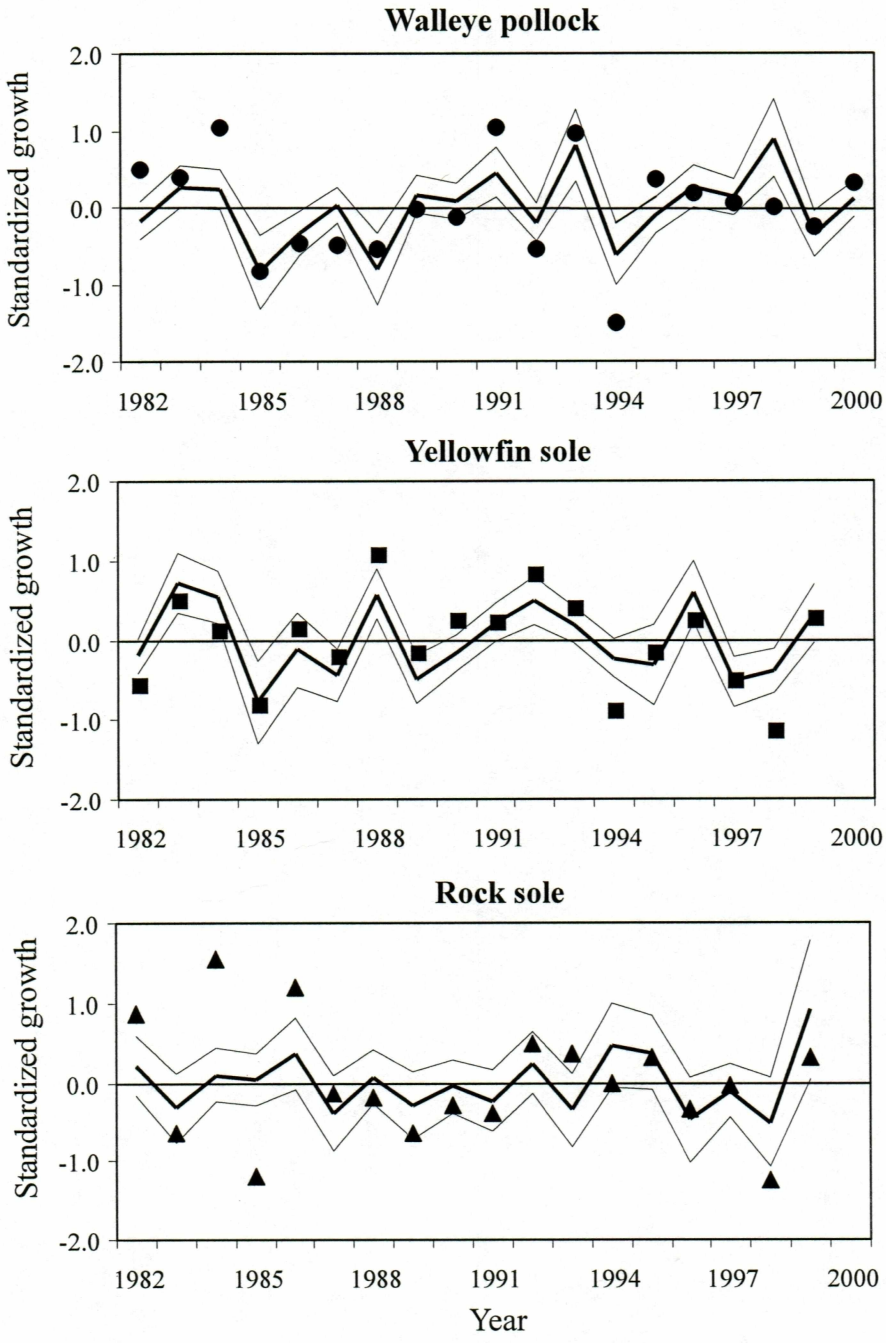

Fig. 8. Stepwise selection model fits for the standardized average growth compared to actual observed growth for pollock (●), yellowfin sole (■) and rock sole (▲). Thin lines represent 95% confidence intervals and heavy lines represent the average standardized growth over the time period.

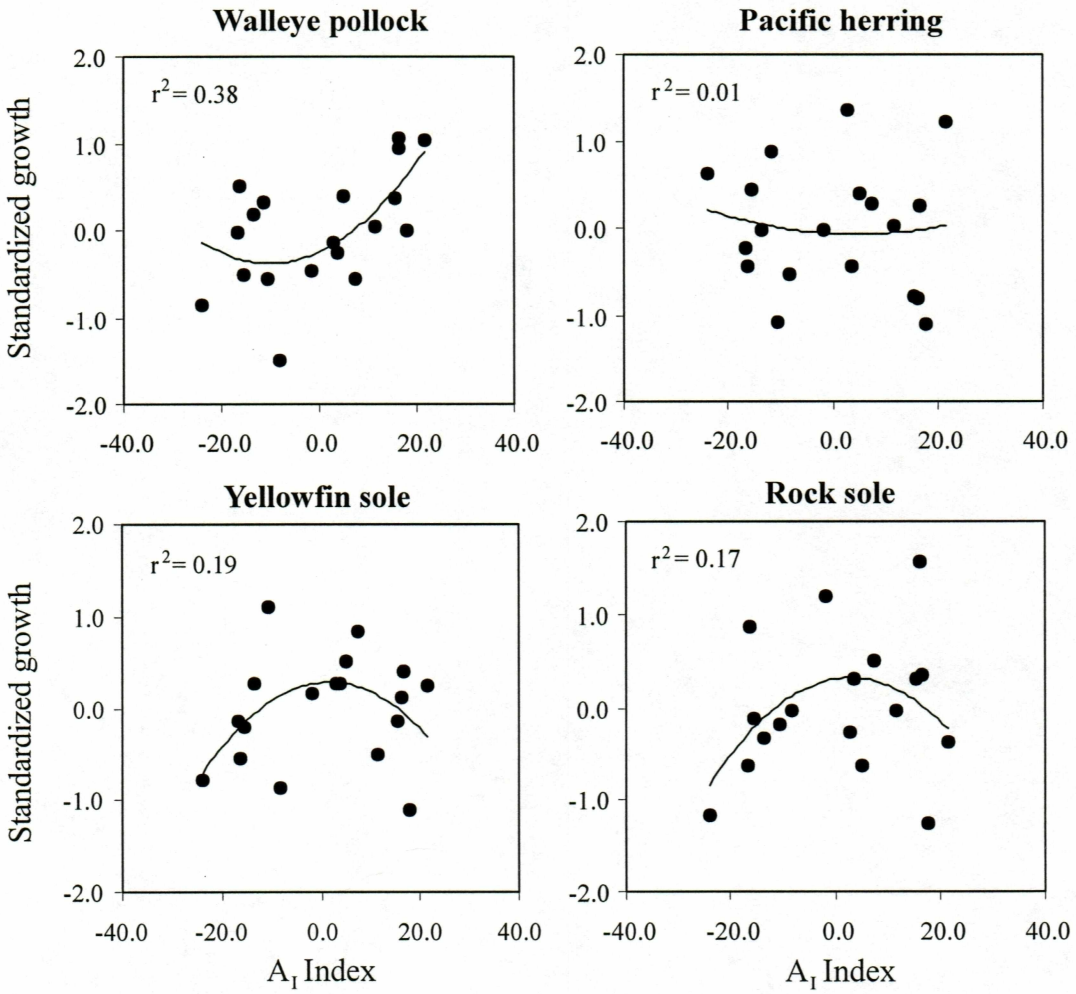

Fig. 9. Standardized growth response of the four study species as a function of the A_I index for the years 1982-2000. Growth for all species shown is growth in length. For pelagic species n = 19 and for benthic species n = 18.

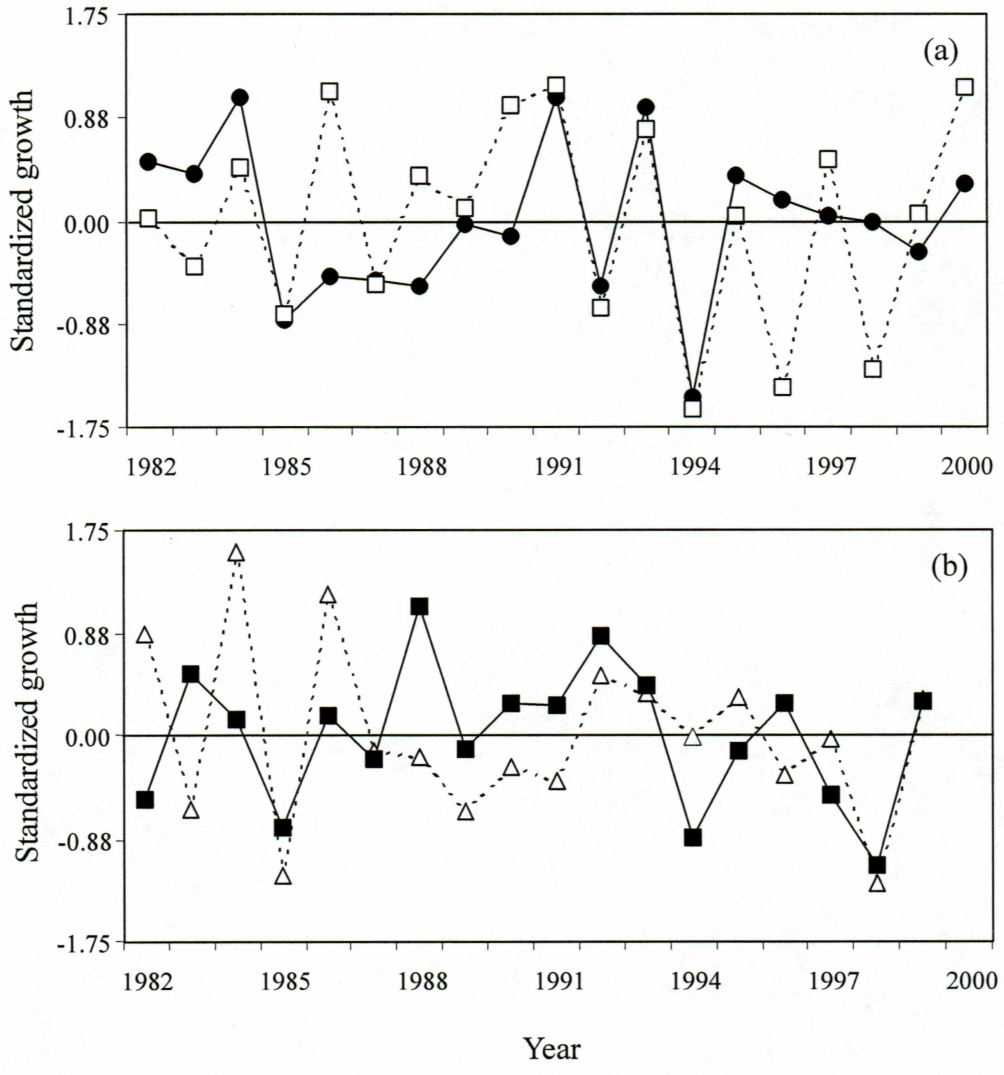

Fig. 10. Comparative annual growth of pelagic (a) and benthic feeders (b). The annual standardized average growths of walleye pollock (●), Pacific herring (measured as weight) (□), yellowfin sole (■) and rock sole (△) are shown.

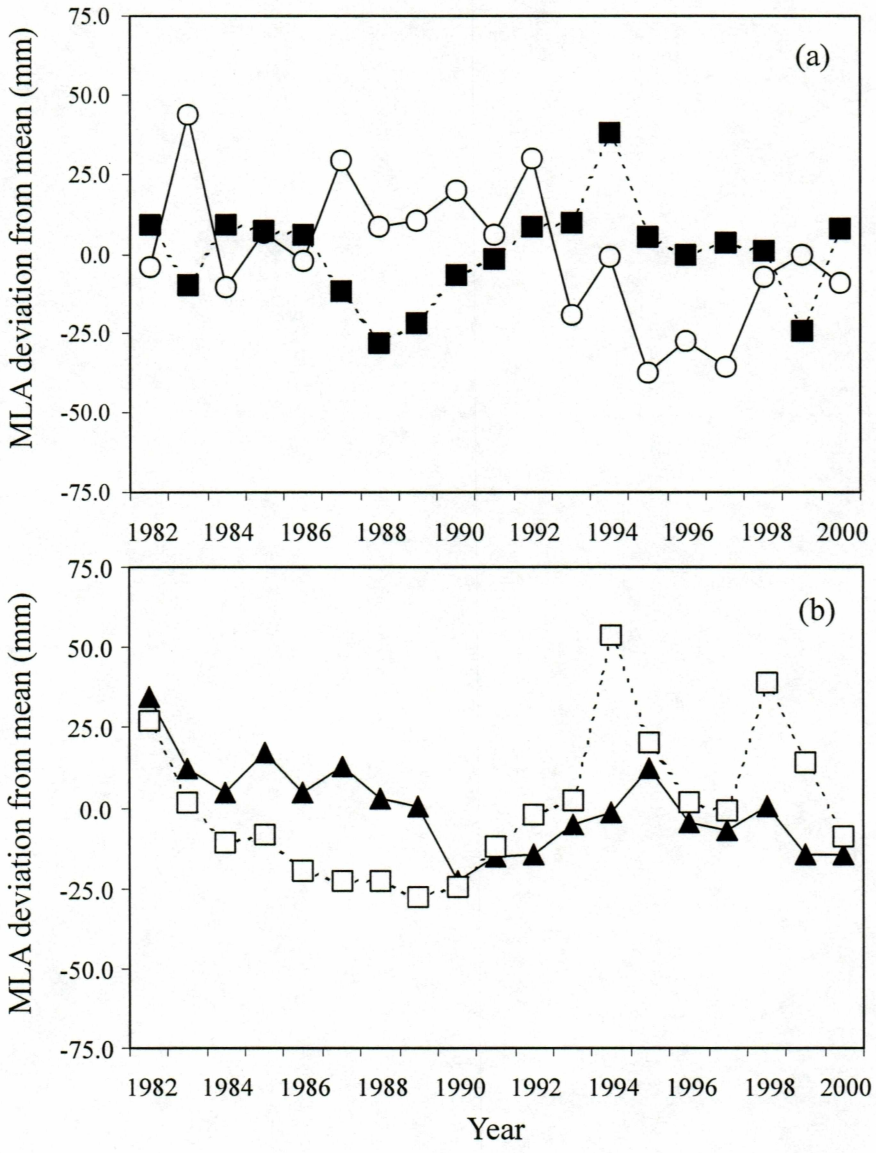

Fig. 11. Comparative plots of the mean length-at-ages for the four study species. (a) Mean length-at-age (MLA) anomalies of age-2 walleye pollock (○) and age-3 yellowfin sole (■). (b) Mean length-at-age anomalies of age-4 Pacific herring (□) and age-3 rock sole (▲).

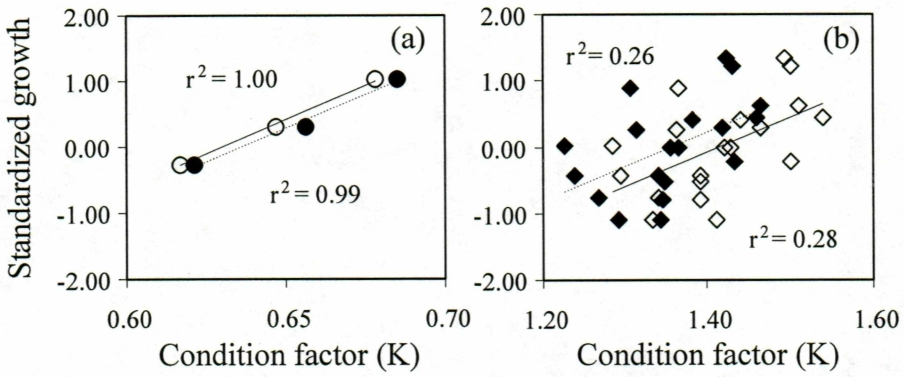

Fig. 12. Walleye pollock (a) and Pacific herring (b) standardized growth regressed against condition factor. The relationship between average standardized growth and condition factor is shown for male (●) and females (○) pollock for the years 1991, 1999 and 2000 and male (◆) and female (◇) Pacific herring for the years 1982-2000.

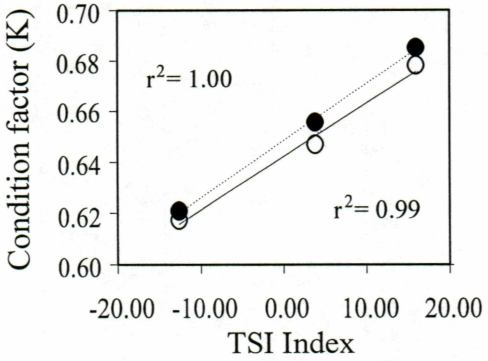

Fig. 13. Pollock condition factor regressed against the TSI index. Regression lines for females (○) and males (●) are shown using data for the years 1991, 1999 and 2000.

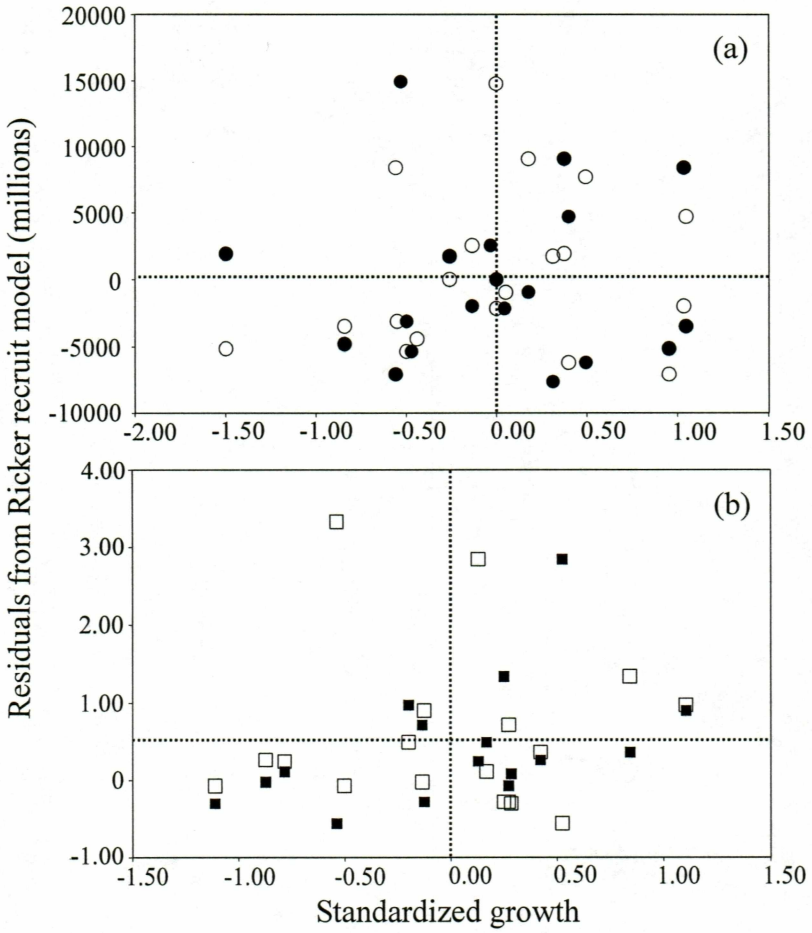

Fig. 14. Relationship of age-2 fish recruitment to standardized adult fish growth for the years 1982-2000. Estimates of number of age-2 fish lagged two years and regressed against standardized growth for pollock (a) and yellowfin sole (b). The recruitment relationship with growth occurring while recruits were age-0 is shown by the solid shapes and age-1 by the open shapes. Average growth and recruitment over the study period (1982-2000) is indicated by dashed lines. Estimates of age-2 abundance obtained from 2002 SAFE reports for both pollock (Ianelli et al., 2002) and yellowfin sole (Wilderbuer and Nichol, 2002).

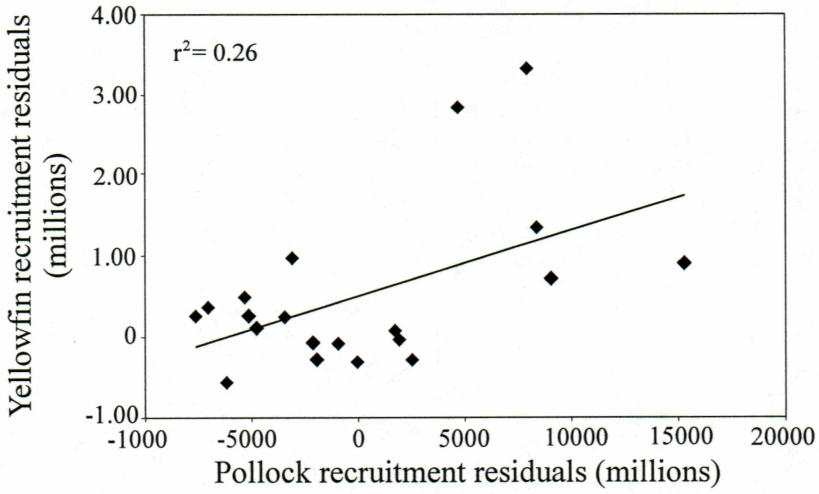

Fig. 15. Relationship of age-5 yellowfin sole recruitment residuals from Ricker spawner-recruit model to the age-2 Ricker spawner-recruit residuals of walleye pollock for the years 1981-2000.

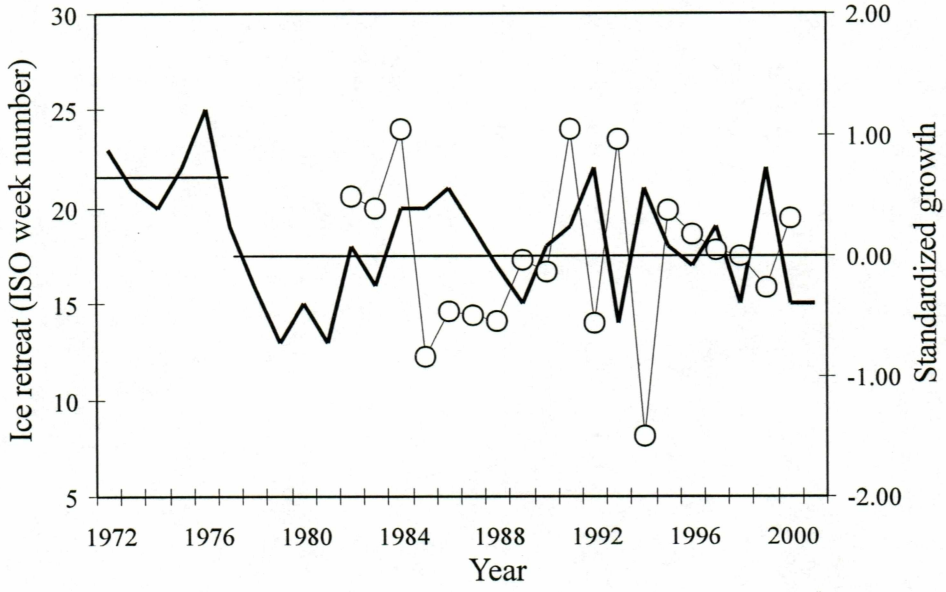

Fig. 16. Comparison of timing of ice retreat (bold line) to annual standardized pollock growth (○). Average dates of ice retreat prior to and after the 1976/77regime shift are shown as horizontal dashed lines.

Table 1. Trophic guilds and species feeding ecology of the four study species. Prey items are listed in order of importance by weight for walleye pollock (Livingston, 1991; Livingston et al., 1993; Livingston and deReyneir, 1996; Lang et al. 2003), Pacific herring (Brodeur and Livingston, 1988), yellowfin and rock sole (Lang et al., 1995).

Trophic guild	Pelagic consumers		Benthic consumers	
Species	Walleye pollock	Pacific herring	Yellowfin sole	Rock sole
Primary location in water column	demersal	pelagic	demersal	demersal
Importance of prey items by weight	juvenile pollock euphausiids misc. fish calanoid copepods	euphausiids calanoid copepods hyperiid amphipods	bivalve mollusks marine worms polychaetes decapod crustaceans	polychaetes marine worms gammarid amphipods misc. fish

Table 2. Eigenvectors and eigenvalues of the first two principal components of monthly sea ice averages (Seasonal Sea Ice index and Temporal Sea Ice index). Percentage of the total variance explained by each principal component is shown.

	SSI (PC1)	TSI (PC2)
$\hat{e}_1$ (Feb)	0.493	0.798
$\hat{e}_2$ (Mar)	0.694	-0.121
$\hat{e}_3$ (Apr)	0.525	-0.590
λ_i	531	281
% Variance	61.3	32.4

Table 3. Relationship between the Temporal Sea Ice Index (TSI) and phytoplankton bloom timing over the middle shelf. Bloom timing was observed at mooring M2 (56.8° N, 164° W) over the middle shelf (Hunt et al., 2002). Negative TSI values indicate late ice retreat.

Year	TSI index	Bloom timing
1999	-12.61	March
1995	-3.56	April
1997	4.52	April
2000	3.93	May
1996	9.47	May
1998	31.90	June

Table 4. Regional shelf water temperature (°C) characteristics and correlation matrix. Mean regional temperatures (± standard deviation) are shown above with correlations (r) between regions and corresponding p-values (in parentheses) shown below.

	Shelf-wide	Outer shelf	Middle shelf	Inner shelf
Average	2.30 ± 0.76	2.87 ± 0.43	1.62 ± 0.80	3.45 ± 1.1
Minimum	0.83	2.04	0.35	0.32
Maximum	3.43	3.67	3.02	4.72

	Shelf-wide	Outer shelf	Middle shelf	Inner shelf
Outer shelf	0.82 (<0.001)			
Middle shelf	0.92 (<0.001)	0.56 (0.014)		
Inner shelf	0.81 (<0.001)	0.52 (0.021)	0.74 (<0.001)	

Table 5. Temperature and timing of retreat characteristics of the A_I sea ice index.

State	SSI-TSI average	SSI	TSI	Shelf surface temperature (° C)	Shelf bottom temperature (° C)	Week of ice retreat (ISO week number)
1	< -10.7	-29.8 (± 7.7)	-2.7 (± 14.5)	6.4 (± 0.5)	2.7 (± 0.5)	16.0 (± 3.7)
2	-10.7 to 3.8	8.8 (± 6.7)	-14.4 (± 12.0)	5.7 (± 1.3)	1.8 (± 0.7)	17.9 (± 2.0)
3	> 3.8	18.7 (± 12.5)	14.3 (± 14.0)	7.3 (± 0.8)	2.6 (± 0.5)	15.4 (± 3.2)

Table 6. Ratios of size-at-age to age-specific growth for the four study species. Ratios are calculated as the average growth over the 19-year study period for the particular age class divided by the mean size-at-age over the same time period and age class.

Age	Walleye pollock	Pacific herring (length)	Pacific herring (weight)	Yellowfin sole	Rock sole
2	4.3				
3	6.1			6.5	4.4
4	13.2	14.1	3.8	5.2	5.2
5	16.9	16.0	4.3	7.3	7.0
6	19.3	19.9	5.2	7.6	8.2
7	21.7	26.7	7.5	11.9	12.4
8	20.8	32.4	9.6	12.2	24.1
9		41.7	13.6	18.6	24.1
10		56.2		23.4	17.0
11		51.2		22.0	
12				30.2	

Table 7. Results of the linear stepwise model selection process. All variables shown are significant at P<0.05. Ages where no significant (NS) models were selected have been grouped together. Positive and negative signs indicate the sign of the variable parameter estimate. For pelagic species n = 19 for all ages and n = 18 for all benthic species.

Species	Age	Significant variables	Model r^2	Model P-value
Walleye pollock	2			NS
	3	Age-0 pollock abundance (+)	0.26	0.025
	4	Age-0 pollock abundance (+), TSI (+)	0.41	0.014
	5			NS
	6	TSI (+)	0.42	0.003
	7	TSI (+)	0.27	0.022
	8	TSI (+)	0.33	0.011
	Age-averaged	TSI (+)	0.50	<0.001
Pacific herring (length)	4	Summer surface temperature (+)	0.46	0.001
	5 - 11			NS
	Age-averaged			*NS*
Pacific herring (weight)	4	Summer surface temperature (+)	0.33	0.010
	5 - 9			NS
	Age-averaged			NS
Yellowfin sole	3	May wind stress (-)	0.28	0.024
	4	May wind stress (-)	0.43	0.003
	5	May wind stress (-)	0.52	<0.001
	6	May wind stress (-), yellowfin abundance (+)	0.52	<0.001
	7 - 8			NS
	9	Zooplankton (-)	0.30	0.018
	10-12			NS
	Age-averaged	May wind stress (-), zooplankton (-)	0.61	<0.001
Rock sole	3	Zooplankton (-)	0.23	0.047
	4	Yellowfin abundance (+), summer bottom temperature (-)	0.48	0.008
	5	Summer bottom temperature (-), summer wind stress (+)	0.42	0.017
	6 - 7			NS
	8	SSI (+)	0.26	0.032
	9	Yellowfin abundance (+)	0.30	0.020
	Age-averaged	Summer bottom temperature (-)	0.26	0.030

Table 8. Correlation matrix of the standardized average growth response for the four study species. Correlations (r) are shown with corresponding p-values below in parentheses. Italicized values are significant at $p < 0.05$. Weight was used as the growth index for Pacific herring. For correlations between pelagic species, n = 19, all others, n = 18.

Trophic guild	Pelagic feeding guild		Benthic feeding guild	
Species	Walleye pollock	Pacific herring	Yellowfin sole	Rock sole
Pacific herring	0.51 (0.027)			
Yellowfin sole	0.22 (0.372)	0.42 (0.085)		
Rock sole	0.25 (0.315)	0.41 (0.090)	0.30 (0.231)	

Table 9. Cross-correlations and significance levels (in parentheses) of spawner-recruit residuals for walleye pollock and yellowfin sole, with standardized adult growth of the representative species. Recruit-residuals were lagged accordingly to correspond with the growth conditions of the particular age.

	Growth period	
	age-0	age-1
Walleye pollock recruitment	0.00 (0.992)	0.17 (0.495)
Yellowfin sole recruitment	0.45 (0.058)	0.01 (0.968)